UNIVERSITY OF CALIFORNIA PUBLICATIONS
IN
ZOOLOGY

Vol. 17, No. 16, pp. 435-504, plates 25-29, 16 text figures May 29, 1918

REVISION OF THE RODENT GENUS *APLODONTIA*

BY

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(Contribution from the Museum of Vertebrate Zoology of the University of California)

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A. INTRODUCTION

1. Prefatory Remarks

Discovered by Lewis and Clark in the early years of the nineteenth century, the peculiar west American rodent genus *Aplodontia* has long attracted interest and attention. It is the sole living representative of that primitive group of rodents, the Aplodontoidea (see Matthew, *in* Osborn, 1910, pp. 534, 535), from which all other mem-

bers of the order have been presumed to be derived, and constitutes a stock which is one of the most conservative known in the class Mammalia. The family to which it belongs (the Aplodontiidae) was the sole mammalian family cited by Wallace (1876, p. 127), as characteristic of his Californian subregion of Nearctica, and is remarkable for its present restricted distribution, being found only on the Pacific coast of North America, in an area which may be bounded roughly by southern British Columbia on the north, the Sierra-Cascade mountain system on the east, and the latitude of San Francisco Bay on the south (see map, text-fig. H).

The unusual characters of the genus *Aplodontia* (see pls. 26, 27), together with the scarcity of fossil remains representative of it, have made the determination of its systematic status a matter of exceptional difficulty. Minding (1829, p. 86) referred the genus *Anisonix* [= *Anisonyx* = *Aplodontia* (part)] to the family Prensiculantia, in which it is associated with twenty-seven other genera, ranging from *Castor*, *Hydromys* and *Mus* to *Bathyergus*, *Tamias* and *Chiromys*. Two years later Bonaparte (1831, p. 20) associated the genus *Aplodontia* with twenty other genera in his "section" Sciurina of the family Muridae. Swainson (1835, p. 388) put *Aplodontia* in his "Division 1" of the Order Glires which contained twenty-two additional genera. By Schinz (1845, pp. 120, 139) the genus was referred to the family Cunicularia, in which were included also arvicolines, octodonts, pocket gophers, and mole-rats. Gervais (1854, p. 364) grouped *Aplodontia* with the pocket gophers. Baird (1857, p. 350) included *Aplodontia* in the subfamily Castorinae; Lilljeborg (1866, opp. p. 9) referred it to the porcupines; Peters (1865, pp. 177, 179), Alston (1876, p. 66, and pl. 4, opp. p. 61), Coues (1877*b*, pp. 543, 601) and others placed it with the squirrels. Gill (1872, p. 22) referred the Haploodontidae to a superfamily Haploodontoidea, listing it as equivalent in rank to the Castoroidea and Sciuroidea; Zittell (1894, p. 523) included the Haplodontidae with certain aberrant families of rodents in his Protrogomorpha; and Thomas (1896, pp. 1014, 1015) accorded to the Aplodontiidae and Anomaluridae separate group rank, leaving it for further research to show their true relationships. The latest classification is that of Matthew and Osborn in 1910, according to which the Aplodontiidae are associated with three extinct families of rodents in the superfamily Aplodontoidea.

Thirteen forms of *Aplodontia* Recent have been described, nine being here recognized. The first formal description was that of

Rafinesque, who characterized "*Anisonyx? rufa*" in 1817 (p. 45) on the basis of Lewis and Clark's account of the sewellel as observed in the neighborhood of the Columbia River. In 1829 Richardson (1829*a*, pp. 333–337) described *Aplodontia leporina* on the basis of specimens collected by David Douglas from within the range of what is now regarded as *Aplodontia rufa rufa*. For thirty-six years no further new names appeared. In 1865 (pp. 177–179) Peters named *Haplodon leporinus* var. *Californicus* from a specimen received at the Berlin Museum, said to have come "aus den Gebirgen Californien." It is the opinion of the writer that this name is tenable for the aplodontia of the Sierra Nevada Mountains of California, which was described by Dr. C. Hart Merriam in 1886 (p. 316) under the name *Aplodontia major*. Four forms of *Aplodontia* were described by Dr. Merriam in 1899*a* (pp. 19–21), as follows: *Aplodontia pacifica*, type locality, Newport, Oregon; *Aplodontia phaea*, type locality, Point Reyes, California; *Aplodontia olympica*, type locality, Quiniault Lake, Washington; and *Aplodontia major rainieri*, type locality, Paradise Creek, Mount Rainier, Washington.

In 1914 two additional forms were described from California: *Aplodontia chrysaola* (here referred to *rufa*), from Jackson Lake, Siskiyou County, by Kellogg (p. 295), and *Aplodontia nigra*, from Point Arena, by the present writer (p. 297). Two years later three more forms were characterized by the writer: *Aplodontia californica columbiana*, from Roab's Ranch, near Hope, British Columbia (Taylor, 1916*c*, p. 499); *Aplodontia rufa grisea* (1916*c*, p. 497, here referred to *rufa*), from the vicinity of Seattle, Washington; and *Aplodontia humboldtiana* (1916*a*, pp. 21–24), from the Humboldt Bay region, California.

2. Material and Acknowledgments

The work here reported upon was begun while the writer was a staff-member at the Museum of Vertebrate Zoology, University of California, and finished after his appointment to the staff of the Bureau of Biological Survey, Washington, D. C. Exclusive of fossil material the present study is based on the examination of 369 specimens, for the most part skins with skulls contained in the collections of the two institutions named.

Through the courtesy of Professor John C. Merriam the writer has had access to the University of California Collections in Vertebrate

Palaeontology, in which are contained some of the most interesting and important specimens known bearing upon the history of the Aplodontiidae and the apparently related fossil family Mylagaulidae.

Acknowledgments are due the following persons: For the loan of additional material for study, to Messrs. F. J. V. Skiff and Wilfred H. Osgood, of the Field Museum of Natural History, Dr. John F. Bovard and Mr. Alfred C. Shelton, of the University of Oregon Museum, and Messrs. Samuel Henshaw and Outram Bangs, of the Museum of Comparative Zoology; for the courtesy of access to the collection under his charge, to Mr. Gerrit S. Miller, Jr., of the United States National Museum; for helpful suggestions regarding the historical problems involved, to Dr. John C. Merriam, of the University of California; for various suggestions in connection with the work, to Messrs. E. W. Nelson, T. S. Palmer, Vernon Bailey, Edward A. Preble, and Hartley H. T. Jackson, of the Biological Survey, and to Messrs. Gerrit S. Miller, Jr., and J. W. Gidley, of the United States National Museum; for a list of vernacular names of *Aplodontia* used by California Indians, to Dr. C. Hart Merriam, of the Harriman Foundation, Smithsonian Institution; and for critical oversight, to Dr. Joseph Grinnell, of the Museum of Vertebrate Zoology, University of California, at whose instance the work was undertaken.

3. Methods of Measurement

All measurements are in millimeters.

Cranial measurements, except where otherwise specified, are taken as follows:

Basilar length: inferior lip of foramen magnum to posterior margin alveolus of incisor.

Length of nasals: most anterior point on nasal bones to most posterior point.

Width of nasals: greatest distance across both of them.

Length of audital tube: outer border of foramen ovale to farthest lateral point (with reference to the skull) on zygomatic (or anterior) side of audital tube.

Length of incisive foramina: greatest length of foramen on right side, that is, with skull resting on its dorsal surface and rostrum pointing away from the observer.

Zygomatic width: greatest inclusive measurement, taken outside of the zygomatic arches.

Greatest width of interpterygoid fossa: at expansion of fossa immediately back of hard palate.

Mastoid width of cranium: greatest inclusive measurement taken outside of mastoid processes.

Alveolar length superior cheek teeth: most anterior point on alveolus of premolar four to most posterior point on alveolus of molar three.

Distance between infraorbital foramina: measured on ventral surface of skull.

Mandible, transversely across angular process: greatest dimension along axis of process, nearly at right angles to axis of mandible itself.

Greatest length of mandible: most posterior point on articular condyle of mandible to most anterior point on alveolus of incisor.

External measurements are ordinarily taken as given below. The short and well-haired tail of *Aplodontia* makes the determination of the total length a matter of some difficulty, in consequence of which this measurement has sometimes been taken on the skinned body instead of as specified below.

Total length, on unskinned body stretched out lengthwise, most anterior point on cartilage of nose to tip of tail, exclusive of hairs.

Hind foot, heel to tip of longest claw.

B. VARIATION IN *APLODONTIA*

1. Age Variation

As the aplodontia grow older the soft gray pelage of the young animal becomes less soft and more brownish or blackish, a ventral brown wash may appear in the adult though seldom in evidence in the young, and the numerous white-tipped hairs which stand out so conspicuously in the pelage of the juvenal become obscured. That specific differentiation takes place early is indicated in several of the subspecies, in none more strikingly, however, than in *Aplodontia rufa nigra*, in which the black coloration of the adult is noted in animals of the year taken in July.

The following tendencies may be observed in the crania as maturity approaches. In dorsal view (pl. 25) all the sutures but those bounding the nasal bones laterally tend to disappear; the interorbital constriction tends to grow narrower, proportionally and absolutely; the temporal lines or ridges become accentuated and approach one another,

though never, apparently, forming a true sagittal crest (the degree of their approach is different in different species); the mastoid processes tend to grow laterad more rapidly than do the audital tubes; the lambdoidal ridge undergoes marked development; the skull becomes more flat, less round, changing from the more squirrel-like form of early youth to the more specialized *Aplodontia* type of full maturity; all processes become accentuated, and the angular process of the mandible undergoes a considerable transverse expansion, its development proceeding at such a rate that the width of the mandible, measured along the axis of this process, increases faster proportionally than does the length of the mandible. Through all these changes the distance anteriorly across the palate between the alveoli of the fourth premolars remains practically constant.

The permanent teeth are long-crowned and as soon as they become somewhat worn afford no clue to age. The tooth formula of *Aplodontia* is $\frac{1}{1}+\frac{0}{0}+\frac{3}{2}+\frac{3}{3}\times 2=22$. Tooth eruption in available specimens is as follows: Superior, milk P^3, milk P^4, M^1, M^2, M^3, permanent P^3, permanent P^4; inferior, milk P_4, M_1, M_2, M_3, permanent P_4.

The fourth premolars (P^4, P_4), are somewhat less specialized in the deciduous dentition than in the permanent. They are brachyodont, somewhat tuberculated, and have deep enamel lakes, in the former; hypsodont, with tuberculation obscure, and with shallower enamel lakes, all trace of which is soon lost by wear, in the latter.

The considerable variation in size of cranium, as well as in the weight of its bars and processes, noticeable in series of fully adult skulls from the same general locality, indicates that slow growth may continue throughout life.

2. Sexual Differences

Aside from a not well-marked tendency toward larger measurements on the part of the males (which, in specimens of *Aplodontia rufa phaea* measured, average eight per cent longer than the females), and the presence of a series of conspicuous ventral markings about the mammae of summer females, practically no differences due to sex can be made out externally. There are in this genus three pairs of mammae. About each, in females in summer pelage, is a nearly circular area of black or dark brown hair ten to twenty millimeters

in diameter, which stands out in strong contrast to the grayish or weakly brownish coloration of the underparts. In males and in winter females the "spot marks" are inconspicuous or lacking.

It would be difficult, if not impossible, to determine the sex of the individual in any given instance by study of the cranium. There is a tendency for ridges and processes to be somewhat more accentuated in the males, for zygomatic arches to be somewhat heavier, and for the temporal ridges to be more closely approximated. Usually the males have basilar length, zygomatic width, mastoid width, and distance transversely across the angular process of the mandible greater than in the females. The largest, heaviest specimens in any adequate series of skulls are usually those of males. In *Aplodontia rufa olympica* the range of variation in size is greater, on the basis of the specimens measured, in the males than in the females. In certain forms the females have the alveolar length of the superior cheek teeth greater than in the males, though the measurements of the latter may exceed those of the former in most respects. In at least two forms, on the basis of measurements taken, the females have interpterygoid fossae averaging broader than in the males. In practically all instances, however, the range of individual variation is so great as to transcend that due to sex.

3. Individual Variation

While in the present study it has been impossible to eliminate geographic, sex, and age variation altogether, still it is believed that the observations, measurements, and percentages given are of value, since they suggest the range of variation, chiefly individual, which must be reckoned with in using a typical series of adults in specific comparisons.

In a series of eleven specimens of *Aplodontia rufa pacifica* taken in February, March and April, there is but little variation in color. Dorsally and laterally all are grizzled pinkish cinnamon, with the brown coloration a little more intense in certain specimens, a little less so in others. The brown wash ventrally varies from near light pinkish cinnamon to pinkish buff. A little more variation, however, is apparent in twelve examples taken during October, November and December. The dorsal coloration in these varies from cinnamon or sayal brown to pinkish cinnamon or light pinkish cinnamon. The pelage of one specimen (no. 9077, Field Mus. Nat. Hist.) is in very

poor condition, suggesting that its aberrant paleness may be due to disease. As with the early spring examples, the uniformity of this late fall series of skins is more noteworthy than the variation observed.

Total length and length of tail vertebrae in this genus, as recorded by the collector, are often unreliable. This follows from the fact that the condition of the tail, which is very short but well-haired, makes accurate measurement of tail vertebrae difficult. The writer has, therefore, put the emphasis in this discussion on the more reliable cranial measurements.

In rodent species with hypsodont teeth the age of adults is determinable not at all or only with difficulty. In such species reliance

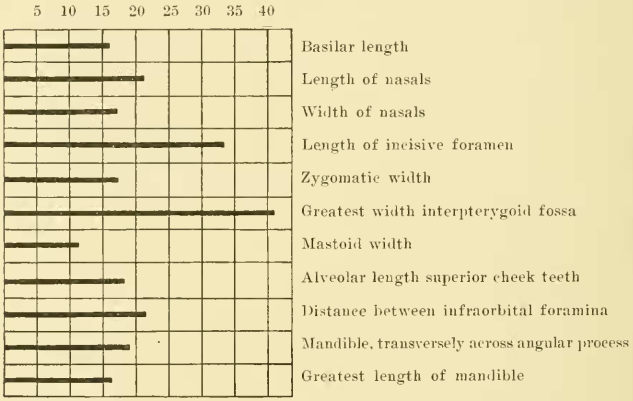


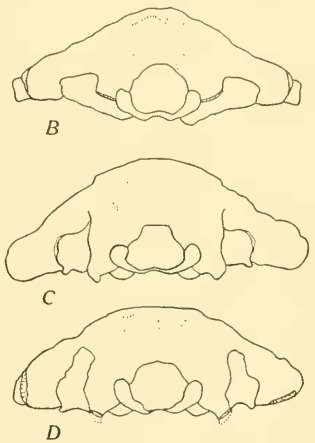
Fig. A. Diagram showing the percentage range of variation (figured on the mean) in cranial measurements of twenty-three skulls of *Aplodontia rufa pacifica* (see table of measurements page 468).

must be placed on the condition of the sutures, the outline of certain bones, the form of the skull, and the development of ridges and processes. It follows that it is possible that an observed range in variation assumed to be individual may really be due to age; and this point ought to be kept in mind through the following discussion.

The diagram (text-fig. A) illustrative of the percentage range of variation shows that for specific comparisons the basilar length, length of nasals, width of nasals, mastoid width, and the width of the mandible, transversely across angular process, are the most dependable characters. Zygomatic width and alveolar length superior cheek

teeth are subject to greater variation, while the length of the incisive foramina, greatest width of interpterygoid fossa, and distance between infraorbital foramina are subject to a considerable range of variation. It is doubtless not an accident that the measurements which, in the nature of the case, can be taken with greatest precision, as basilar length and mastoid width, appear to be subject to less variation than those which are more difficult to take with entire accuracy.

The outline of the nasals is fairly uniform in the entire series, the small variation observable being in the condition of the shallow embayment in the lateral outline of the nasals posteriorly, and in their relative breadth anteriorly and posteriorly. The width of the inter-



Figs. B–D. Posterior view crania of *Aplodontia rufa pacifica*, to illustrate variation in relation of parts. × 1. Fig. B, no. 89309, Biol. Surv. Coll.; fig. C, no. 9052, Field Mus. Nat. Hist.; fig. D, no. 77371, Biol. Surv. Coll.

orbital constriction is highly variable, not only in animals of different ages, but also in animals of apparently similar age. In certain specimens a little rounded notch is developed in the lachrymal region, on the anterior border of the orbit. In others, this notch is feebly developed or lacking entirely. The degree of development and approach of the temporal lines or ridges is variable. In some specimens the ridges are weakly developed and comparatively far apart, in others strongly developed and much closer together. The weight of

the zygomatic arch is often different in animals of apparently the same age. The arches are bowed outward more in some specimens than in others. The postzygomatic notch is variable. The degree of development of the lambdoidal crest varies in animals of apparently comparable age, being accentuated in certain specimens and setting off a considerable fossa anterior to it, but in others being comparatively weakly developed.

Perhaps the most variable of the cranial characters are furnished by the bones on the posterior aspect of the skull (see text figs. B, C, D). In the adult, the sutures between the exoccipitals, supraoccipital, and the basioccipital have completely disappeared. The paroccipital process and the occipital condyle belong to the exoccipitals. The substance of the mastoid process, as viewed on the posterior aspect of the cranium, results from the ankylosis of two elements, one, the inner, from the exoccipital, and the other, the outer, from the squamosal. A plate from the latter bone invades the outline of the mastoid process from below, and is marked off by prominent sutures in animals of every age. The degree of expansion of the winglike mastoids, the degree of development of the paroccipital processes, and particularly the degree of invasion of the plate of the squamosal which comes up from below, are subject to variation, the wide range of which suggests that it may be due to age. Individual differences are observable in the outline of the foramen magnum, which is rounder in some specimens, flatter in others. In the ventral aspect of the skull one notes that there is considerable variation in the diameter of the third upper premolar, and noticeable variation in the outline of the hamular processes, the length of the incisive foramina, the outline of the interpterygoid fossa, the outline of the zygomatic arch particularly posteriorly, the caliber of the audital tubes and the degree of expansion and development of the paroccipital processes. The relations of the foramina in the regions of the foramen lacerum medium are subject to much variation.

Looking at the skulls in their anterior aspect it is of interest to note the variation in size of the infraorbital foramen, which in its greatest diameter, ranges, in different specimens, from about 2.6 to 4.0 millimeters.

The outline of the coronoid process of the mandible varies from a form in which it is scarcely hooked backward at all, to one in which the hook form is prominent. The mass and outline of the condylar process undergo considerable change from one individual extreme to

the other. The inner and outer prominences of the broad angular process of the jaw are differently outlined in different specimens, and the ridge extending from the inner prominence of the angular process exteriorly on the jaw to bound the masseteric fossa anteriorly is comparatively well developed in certain specimens, whereas in others it is interrupted by a smooth space.

4. Molt and Seasonal Variation

There is but one molt annually in *Aplodontia*. Pelage renewal begins in July and August, rarely as early as June, and continues for two or three months. There is no hard and fast manner of molting. The hair usually begins coming in on the sides posteriorly and on the back of the head and neck about the same time. From these centers the molt spreads until the new pelage covers the body, the hair of the shoulders and rump being the last to be renewed dorsally. In some examples the molt proceeds somewhat irregularly. The molt of the underparts lags behind that of the upperparts. Additional details as to molt are mentioned in the accounts of species and subspecies.

The new pelage is longer and sometimes slightly different in coloration from the worn pelage it replaces. Thus in *Aplodontia rufa pacifica*, the fresh pelage is more richly colored than the worn pelage; in *A. r. californica*, it is a trifle browner; and in *A. r. phaea*, it is a little more intensely colored. Differences in coloration and general appearance are small, however, and in several forms of *Aplodontia*, as at present represented in the collections examined, cannot be shown to exist at all.

5. Geographic Variation

Geographic variation, like time variation, is comparatively slight in the genus *Aplodontia*. The forms are so little differentiated that variation geographically is often obscured by individual variation. All of the described forms may with entire propriety be referred to a single species.

Mountain forms are larger as a rule than nearby lowland or coastal forms. Thus *Aplodontia rufa columbiana* of the mountains of Hope District, British Columbia, tends to be larger than *A. r. rufa* of the Puget Sound region; in like manner *rainieri* from Mount

Rainier, Washington, averages larger than *rufa;* and *californica*, inhabiting the Canadian zone of the Sierra Nevada-Cascade mountain system in California, is considerably larger than *phaca*, found in the coastal Marin County near San Francisco Bay. Although this tendency toward variation in size is slight, its apparently uniform association with difference in altitude or life-zone indicates its possible significance.

It has been considered (C. Hart Merriam, 1899*a*, p. 21; Taylor, 1916*c*, p. 501) that the "mountain top" subspecies of *Aplodontia* (*columbiana*, *rainieri*, *californica*) are more closely related to each other than to any other forms of the genus. This is possibly true of *columbiana* and *rainieri* (see pl. 28), but the balance of the evidence, as derived from the present study of *rainieri* and *californica*, favors rather the view that these mountain subspecies are more closely related to lowland or neighboring forms than to each other. Their general similarity in size and certain other characters would seem to be due to parallelism.

Geographic isolation appears to be intimately associated with speciation in the group. Although material at hand is not sufficient to demonstrate each step in the process, it is enough to suggest that the ranges of all the described subspecies of *rufa*, except *nigra* and *phaca*, inosculate at one point or another. Geographic variation is continuous, though slight and very gradual, in the intergrading forms. The most strikingly colored form is the apparently completely isolated *Aplodontia rufa nigra* of Point Arena, California.

It is to be noted that whereas on the northern coast of California three well-marked forms of *Aplodontia* are found, on a longer coastline in the state of Oregon there occurs but one. The three communities of *Aplodontia* on the coast of northern California are separated from each other by considerable gaps, while along the coast of Oregon the animals appear to be continuously distributed.

It seems to the writer that the geographical distribution of the different subspecies of *Aplodontia*, as well as the degree of development and nature of the characters separating them, indicate that among the factors possibly concerned in their differentiation, geographic isolation is, at least, one of the most important.

C. HISTORY OF THE APLODONTIIDAE

1. General Remarks

This family is exclusively North American in origin, development, and present distribution. In the absence of any other evidence of European relationship it is probable that the resemblances noted between the American Oligocene aplodontid genus *Allomys* and the genus *Sciurodon* of the European Oligocene (see Schlosser, 1884, pp. 73, 136) are indicative of accidental convergence rather than real relationship.

The earliest aplodontid genius is *Allomys* Marsh (1877, p. 253) or *Meniscomys* Cope (1878, p. 5). Found typically in the Oligocene deposits of the Middle John Day in Oregon, there is only a single record, so far as known to the writer, of its occurrence elsewhere, that of Matthew (1904, p. 263), who has recovered an undetermined species from the Lower Miocene of South Dakota.

The members of the genus *Allomys* were small, ranging from one-half to two-thirds the size of Recent *Aplodontia*. They were much more squirrel-like than is the Recent genus.

Founded upon a single specimen, an imperfect cranium without lower jaws, taken in the gravels and tuffs at the top of the Upper John Day, *Mylagaulodon* is one of the most interesting of the genera which are associated with the Aplodontiidae. The characters of the fourth premolar and infraorbital region of this genus are regarded as demonstrating its aplodontid position.*

The earliest known fossil remains of the genus *Aplodontia* were found by parties from the University of California in the Virgin Valley Miocene and Thousand Creek Pliocene of northern Humboldt County, Nevada. The species there recovered is known as *Aplodontia alexandrae* Furlong (1910, pp. 397–403). It is somewhat smaller than the Recent members of the genus, and differs from them in several particulars, the most important being the relative position of the prominent style internally on the lower molars. For all that, one is impressed with the resemblances rather than the differences between the Tertiary *Aplodontia alexandrae* and the Recent species of the genus.

Another species of *Aplodontia* has recently been described by Dr. J. C. Merriam (1916, pp. 177–179) from the Cedar Mountain region of western Nevada. The formation in which the specimen (a single

upper premolar four, somewhat broken) was found has been referred to the Upper Miocene (*loc. cit.*, p. 171), the Cedar Mountain fauna being regarded as intervening in time between the Mascall Middle Miocene of the Middle Basin area and the Barstow Upper Miocene of the Mohave area.

That both *Aplodontia alexandrae* and the Cedar Mountain species represent advanced stages of development between *Allomys* and *Aplodontia* seems clear. Both are nearer *Aplodontia* than *Allomys;* but neither one is so specialized as are the Recent forms of *Aplodontia.*

There remains to be considered only *Aplodontia major fossilis* Sinclair (1905, pp. 147–148), discovered in 1902 by an expedition from the University of California, in the Pleistocene Potter Creek Cave, Shasta County, California. Comparison of the numerous remains of this species in the University of California Collections in Vertebrate Palaeontology with a large series of skulls and jaws of *Aplodontia rufa californica*, the Recent form occurring in the same general region, shows that the Pleistocene form is very doubtfully if at all distinguishable from the living species.

2. Summary and Discussion

It is worthy of remark that nearly all of the records of extinct members of the family Aplodontiidae are from the now arid territory east of the great Cascade-Sierra mountain system, which system, at the present time, marks the eastern boundary of the range of the genus (see map, text-fig. E). The members of the chiefly Oligocene genus *Allomys* hail from the John Day Beds of eastern Oregon, with one outlying undetermined species in the Rosebud Lower Miocene of South Dakota; *Mylagaulodon* comes from the top of the Upper John Day in eastern Oregon; *Aplodontia alexandrae* occurs in the arid Virgin Valley and Thousand Creek beds of northern Humboldt County, Nevada; an *Aplodontia* of an unnamed new species comes from the Cedar Mountain region of western Nevada; and only *Aplodontia major fossilis*, found in the Pleistocene Potter Creek and Samwel caves, in the Shasta region of northern California, comes from the Pacific slope of the Sierran system. Apparently the range of the family Aplodontiidae, as well as of the genus *Aplodontia*, was formerly much greater than at present, though it must be conceded that very little is known of the precise relationships of the early aplodontids to the Recent genus, and we have little data on the westward range of members of the family in Tertiary time.

Reference has already been made to the conservatism of the aplodontid phylum. If, as seems highly probable, *Aplodontia alexandrae* is near the direct line of descent of the recent species, it is noteworthy that, during a lapse of time sufficient for the evolution of the horse from the Miocene *Merychippus* type to the larger Pliocene *Pliohippus*, there was no great specific change; and that, during a time which sufficed to transform the short-toothed, small-sized *Merychippus* into the much larger modern *Equus*, with modifications in every bone in the body, and with characters generically probably twice removed, the aplodontid stock has undergone comparatively slight change, all

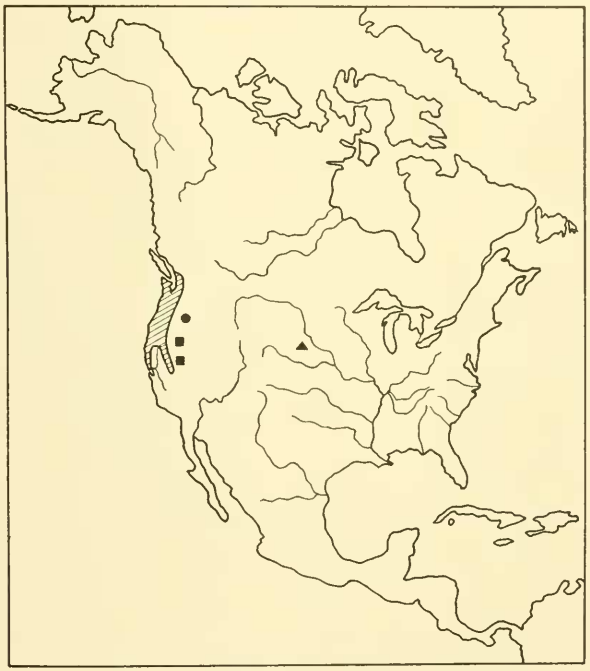


Fig. E. Continent of North America, to indicate present range of genus *Aplodontia*, and apparent extension of range of family Aplodontiidae in Tertiary times.

Cross-hatched area indicates limits of range of Recent genus; circle represents record of fossil genera *Allomys* and *Mylagaulodon;* triangle indicates an additional record of *Allomys;* squares indicate records of genus *Aplodontia* fossil.

observed variations, as at present recognized, falling within the limits of a single genus.

D. HABITS OF *APLODONTIA*

Aplodontia is herbivorous, colonial, nocturnal, and fossorial. A considerable degree of humidity and an abundant supply of food plants seem to be necessary conditions to its existence. Situations well sheltered by a tangle of vegetation are usually chosen for its burrows. Its nest is made underground, in an enlarged chamber. Attention has been called to a hay-making instinct. The "hay" consists simply of green plants of various kinds cut up and spread out as if to dry and to be used later. Sight and hearing are apparently defective; but smell and touch, particularly the latter, appear to make up for any deficiencies in these respects.

Little is known of the animal's breeding activity. Young have been taken throughout the summer season. It has been asserted that *Aplodontia* has a shrill cry. Among its enemies are weasels, skunks of two genera, wildcats, mink, gray foxes, golden eagles and great horned owls. Other potential enemies are coons, badgers, and fishers.

Although locally *Aplodontia* does some damage to man's interests, its habitat is such that for the most part it is of no economic significance. It burrows holes in ditch walls along the line of the Southern Pacific in the Sierra Nevada in California; in Oregon it undermines government trails, causing them to be washed out; and Lantz (1917, p. 16) reports that in western Washington considerable complaint has been made of their depredations on crops, particularly small fruits. The skins are of little or no value.

The habits of *Aplodontia* have recently been studied by Anthony (1915, pp. 53–63). The most complete paper on this subject to date is that of Mr. Charles Camp, now in press in this series of publications.

E. PRESENT SYSTEMATIC STATUS OF *APLODONTIA*

1. The Family Aplodontidae

Prensiculantia (part) Minding (1829), p. 86.
Muridae (part), Bonaparte (1831), p. 20.
Sciuriua (part), Bonaparte (1831), p. 20.
Cunicularia (part) Wagner (1843), pp. 357, 395.
Pseudostomides (part) Gervais (1854), p. 364.

Saccophoriens (part) Gervais (1854), p. 364.
Sciuroides (part) Brandt (1855), p. 151.
Haploodontini or Prismatodontes Brandt (1855), p. 151.
Sciuridae (part), Baird (1857), pp. 240, 350.
Castorinae (part) Baird (1857), p. 350.
Haploodontidae Lilljeborg (1866), table opp. p. 9.
Haploodontoidea Gill (1872), p. 22.
Haplodontidae Alston (1876), pp. 66, 75, 78.
Haplodontiidae Cope (1883), p. 54.
Aplodontidae Allen (1892), p. 31.
Aplodontiae Thomas (1896), p. 1015.
Aplodontiidae Thomas (1896), p. 1015.
Haplodontoidea Weber (1904), p. 496.
Aplodontoidea Matthew, *in* Osborn (1910), p. 534.

Characterized by Matthew (1910, p. 69) as follows:

"Teeth $\frac{1.0.2.3}{1.0.1.3}$, progressively hypsodont, with prominent mesostyles and metastylids. No postorbital process; zygomatic arch slender; skull wide posteriorly; postero-inferior portion of angle greatly inflected, posterior end everted. Fossorial, Oligocene to recent. Genera, *Aplodontia, Meniscomys* [= *Allomys*], *Mylagaulodon.*"

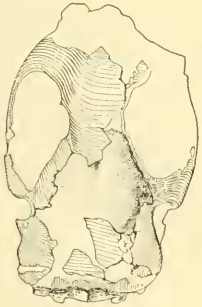


Fig. F

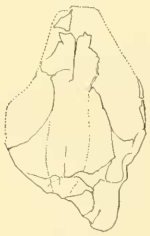


Fig. G

Fig. F. *Allomys liolophus* Cope, dorsal view of cranium. × 1. Univ. Calif. Coll. Vert. Palae., no. 1672; locality 898, John Day Beds, Oregon.

Fig. G. *Allomys cavatus* Cope, dorsal view of cranium. × 1. Univ. Calif. Coll. Vert. Palae., no. 1444; locality 864, John Day Beds, Oregon.

If *Allomys* is to be referred to the family Aplodontiidae a change in the above characterization will be necessary; for postorbital processes are present in specimens of *Allomys liolophus* and *A. cavatus* in the University of California Collections in Vertebrate Palaeontology (see text-figs. F, G).

2. The Genus *Aplodontia*

The chief generic characters are as follows: dentition $\frac{1}{1}+\frac{0}{0}+\frac{2}{1}+\frac{3}{3}\times 2=22$; permanent teeth hyposodont, of secondarily simple enamel pattern, characterized by prominent styles internally on the inferior teeth and externally on the superior teeth; cranium greatly depressed; postorbital processes on frontal absent; postorbitals on jugal weakly or not at all developed; infraorbital foramen primitive, not transmitting any part of masseter; angle of mandible remarkably expanded transversely; scaphoid and lunar not separate; fibula not articulating with calcaneum, free from tibia; body stout, about 350 millimeters long; pelage dark; eyes and ears small (pl. 29); mammae six; tail very short; nocturnal, fossorial, found in restricted area in western North America.

The much modified hyposodont teeth, the depressed skull, the absence of postorbital processes (pls. 26, 27), the extraordinarily inflected angle of the mandible, the fusion of the scaphoid and lunar into a single bone, the proportionate enlargement of the forefeet (for digging), and probably also the smallness of eyes and ears, are suggestive of a high degree of specialization in *Aplodontia*. On the other hand the simplicity of the dental formula and the characters of the infraorbital region (pl. 27) show a generalized or primitive condition. The infraorbital foramen is moderate in size, and does not transmit any portion of the masseter, the origin of which, according to Matthew (1910, p. 69), is wholly behind and below the lower margin of the orbit, and not extended forward on the side of the muzzle.

3. Variations in the Generic Name

Palmer (1904, pp. 24, 25) has called attention to the fact that the name *Aplodontia* is capable of twenty-four modifications, each one progressively differing from the next by a single letter. That several of these possible spellings of the name have found place in literature is indicated by the following list of names applied to the genus:

Anisonyx (part) Rafinesque (1817), p. 45.
Anisonix (part) Minding (1829), p. 86.
Aplodontia Richardson (1829*a*), pp. 333–337.
Aplndontia Fischer (1830), p. 398 (error for 598).
Haplodon Wagler (1830), pp. 4, 22.

Aretomys (part), Douglas (1914), pp. 59, 156.
Aplnodontia Richardson (1837), p. 150.
Aplodontie Gervais (1854), p. 364.
Haploodon and Hapludon Brandt (1855), p. 150, footnote.
Haploödon, Haploudon, Haploödus, Haplodus, Haploudus Coues (1877*b*), p. 556.
Haplodonta Cope (1883), p. 55.
Hapludus, Aploudontia, Haploudontia Coues (1890), p. 2712.
Haplodontia Elliot (1899), pp. 241–276.
Aploodontia, Aplodon, Aploodon, Aploudon, Apludon, Aplodus, Aploodus, Aploudus, Apludus, Haploodontia, Hapludontia Palmer (1904), p. 25.

There has been no agreement as to a vernacular name for aplodontia. Among names applied to the animal are found the following: Mountain beaver, mountain boomer, gehalis, and farmer; giant mole, mammoth mole, ground bear, marmot, ground hog, woodchuck, gopher, badger, muskrat, blue muskrat, high ground muskrat, and (Indian names) sewelel, shewelel, sewewel, or sewellel, showhurll, showhurtl, showtl, showt'l, show'tl, shote, squallah, swak-la, o-gwal-lal, and ou-ka-la. I am indebted to Dr. C. Hart Merriam for the following list of names given aplodontia by certain tribes of Californian Indians:

Name	Tribe	Locality
Ne-ta-te	Tolowa or Huss	Crescent City
Mah-pe-neetch	Karok	Happy Camp to Weitzpek
Tabt-ka-wer-itl	Soo-lah-te-luk	Humboldt Bay
Waw-kaw-see	Mo-des-se	Pit River
Yah-sah	Nis-se-nan	Colfax and Placerville to Yuba
Wes-skap[e]	Yurok	Lower Klamath; mouth of river to Weitzpek

4. List of Species and Subspecies with Type Localities

Aplodontia rufa rufa (Rafinesque). "Neighborhood of the Columbia River"; specimens from Marmot, Clackamas County, Oregon, regarded as typical. (p. 454)

Aplodontia rufa olympica Merriam, C. H. Quiniault Lake, Chehalis County, Washington. (p. 460)

Aplodontia rufa columbiana Taylor. Roab's Ranch, near Hope, British Columbia. (p. 463)

Aplodontia rufa rainieri Merriam, C. H. Paradise Creek, south side of Mount Rainier, Washington. (p. 465)

Aplodontia rufa pacifica Merriam, C. H. Newport, mouth of Yaquina Bay, Lincoln County, Oregon. (p. 467)

Aplodontia rufa humboldtiana Taylor. Carlotta, Humboldt County, California. (p. 470)

Aplodontia rufa californica Peters. The mountains of California; assumed to be the Sierra Nevada; specimens from Blue Canyon regarded as typical. (p. 473)

Aplodontia rufa nigra Taylor. Point Arena, Mendocino County, California. (p. 479)

Aplodontia rufa phaea Merriam, C. H. Point Reyes, Marin County, California. (p. 480)

5. Accounts of Species

Aplodontia rufa rufa (Rafinesque)

Brown Aplodontia

Sewellel Lewis and Clark (1814), p. 176.
Sewewell [=*Sewellel*] Lesson (1827), p. 240.
Ground Rat Douglas (1836), p. 101.
Arctomys brachyurus? Douglas (1836), p. 101.
Anisonyx? rufa Rafinesque (1817), p. 45.
Anisonyx? rousse Desmarest (1822), p. 330.
"*Anisonix rufa?*" Minding (1829), p. 86.
Arctomys rufa, Harlan (1825), pp. 308–309.
Anisonyx roux Lesson (1827), p. 240.
Aplodontia leporina Richardson (1829*a*), pp. 333–337.
Apludontia leporina, Fischer (1830), p. 398 [=error for 598].
H[aplodon]. leporinus Wagler (1830), p. 22.
Apluodontia leporina Richardson (1837), p. 150.
Aplodontie léporine Gervais (1854), p. 364.
H[aploodon]. leporinus, Lilljeborg (1866), p. 41.
Haplodon rufus Coues (1877*b*), p. 557.
Haplodonta rufa, Cope (1883), p. 55.
Aplodontia rufa, Merriam (1886), pp. 312–328.
A[plodontia]. rufus, Price (1894), p. 328.
Aplodontia major (part) Merriam (1897), p. 219.
H[aplodontia]. rufa, Elliot (1899), p. 251.
Aplodontia chryseola Kellogg (1914), pp. 295–296.
Aplodontia rufa grisea Taylor (1916*c*), pp. 497–499.

Type Locality.—It is well known that Rafinesque's description of "*Anisonyx? rufa*" was based entirely upon the Sewellel of Lewis and Clark. As cited by Rafinesque the type locality is the "neighborhood of the Columbia River." It is now known that two subspecies of *Aplodontia* occur on the Columbia River. The coastal form described as *Aplodontia pacifica* is found at Astoria, while an inland form commonly known as *A. rufa* occurs in the foothill country about Mount Hood. The original description of *rufa* is not diagnostic as between the coastal and the inland forms. Doubtless Lewis and Clark saw Indian robes made from the skins of both. There would be no

advantage in transferring the name *rufa* to the well known form *pacifica*. It seems altogether appropriate, on the other hand, that the name *rufa* be fixed on the inland race, of which specimens collected at Marmot, Clackamas County, Oregon (western slope of Mount Hood, not far from the Columbia River), may be regarded as typical.

Specimens Examined.—Total number, 135, from the following localities:

British Columbia: New Westminster Provincial District—Chilliwack, 5; Sumas, 1; Mt. Baker Range, 1.

Washington: Skagit County—Sauk, 8 (1 skull only); Hamilton, 1; Mt. Vernon, 5 (2 skulls only). King County—Seattle, 6 (one is skull and skeleton only); Ravenna, near Seattle, 1; Renton, near Seattle, 3; Kirkland, 6; "Puget Sound"?, 2. Kittitas County—Easton, 8. Pierce County—Puyallup, 2.

Oregon: Clackamas County—Marmot, 6 (2 skulls only); Eagle Creek, eight miles southeast of Bissell, 1; Bissell, 1; head of Eagle Creek, 1; "Clackamas County," 1 (no skull). Lane County—Vida, 6; McKenzie Bridge, 3; Horse Pasture Mt., ten miles by road southeast of McKenzie Bridge, 3; O'Leary Mt., ten miles by road southeast of McKenzie Bridge, 1. Jackson County—Siskiyou, 20; north base Ashland Peak (alt. 5,200 ft.), 2. Klamath County—Mt. Mazama, Anna Creek (alt. 6,000 ft.), 3; Fort Klamath, Anna Creek Canyon, 3.

California: Siskiyou County—Siskiyou Mts., White Mt. (alt. 6,000 ft.), 8; Siskiyou Mts., Craigy Peak (alt. 6,200 ft.), 1; Siskiyou Mts., Studhorse Canyon (alt. 6,500 ft.), 1; Trinity Mts., east of Hoopa, ten miles west of Forks of Salmon (alt. 5700–5,800 ft.), 5; Salmon Mts., Etna Mills, 3; Salmon Mts., Jackson Lake, 5; Salmon Mts., Wild Cat Peak, 1; Salmon Mts., South Fork of Salmon River, 1. Trinity County—Canyon Creek, 5; Salmon

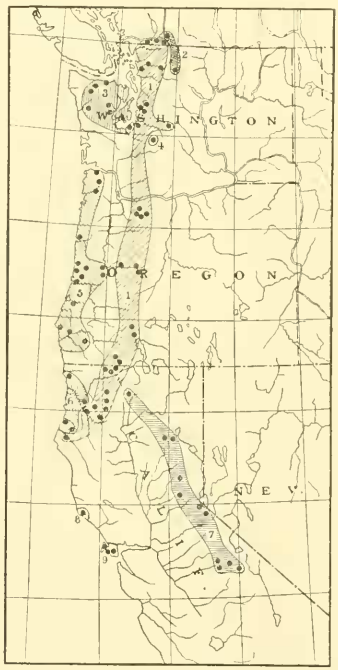


Fig. H. Geographic distribution of the nine recognized races of the genus *Aplodontia*.

1. *Aplodontia rufa rufa*
2. *Aplodontia rufa columbiana*
3. *Aplodontia rufa olympica*
4. *Aplodontia rufa rainieri*
5. *Aplodontia rufa pacifica*
6. *Aplodontia rufa humboldtiana*
7. *Aplodontia rufa californica*
8. *Aplodontia rufa nigra*
9. *Aplodontia rufa phaea*

Mts., head of Grizzly Creek, 3. Humboldt County—"Northwest California" [Hoopa Valley], 2 (no skulls); Rio Dell, 1.

Geographic Range.—Neighborhood of the Columbia River, in western Oregon, interiorly on the Pacific side of the Cascades; thence southward in a belt of unknown width to Mount Mazama in southern Oregon and the Siskiyou-Trinity district in northern California; northward to Puget Sound and the Chilliwack-Sumas region in southwestern British Columbia. Altitudinal range, from sea level in the Puget Sound district to 6,500 feet in the Siskiyou-Trinity Mountains of northern California; zonal range, Transition and Canadian.

Cranial Characters.—Skulls moderate (see measurements below), nasals variable in outline, broad anteriorly, but usually much narrowed at their posterior ends; rostrum short; audital tubes in typical material tending to be of greater caliber than in other forms of the genus, about as in *californica* (see Remarks, below).

External Characters.—Above, in specimens taken at all seasons, light ochraceous-buff (Ridgway, *Color Standards and Color Nomenclature*, 1912), in some specimens grading anteriorly into light buff, vinaceous-cinnamon or even occasionally approaching tawny; some with a distinctly grayish, others a distinctly brownish cast of coloration; some examples paler anteriorly and grayer posteriorly, with deepest coloration in middle region of body; grizzled with more or fewer blackish hairs; white spot at base of ear; some silvery-white hairs insprinkled, particularly posteriorly. Below, grayish, with the faintest possible wash of brownish of a hue near pinkish buff, or brownish, with a conspicuous wash of vinaceous-cinnamon or light vinaceous-cinnamon, and with scattered black hairs insprinkled; practically all hues between these are observable; drab-gray basal coloration showing through to a greater or less degree; spot-marks about mammae in spring and fall females seal brown or paler in coloration.

Molt and Seasonal Change.—That *Aplodontia rufa rufa* molts once, that the pelage renewal takes place during the late summer and the fall, and that a term of from two to three months is required for the completion of the molt, is suggested by the following facts: Specimens taken May 17, June 5, 22, 23, and July 22 and 23, and even two exceptional specimens taken August 26 and September 13, are much worn but show no sign of molt. On the other hand, molt has already begun in other specimens of *rufa* taken on June 23 and 24, and pelage renewal is going on in practically all specimens taken during August, September and October. Examples secured Septem-

ber 29 and October 9, respectively, show the last stages of the process; and the molt is entirely completed in a specimen taken November 21. Evidently August, September and October are the principal months of molt.

Seasonal changes are trifling. The fresh pelage is longer and tends to be somewhat browner, sometimes blacker, than in its hold-over stage in spring and early summer.

Cranial Measurements of *Aplodontia rufa rufa* (13 Skulls) From Marmot, Vida and Vicinity of McKenzie Bridge, Oregon

	Average	Mean	Maximum	Minimum
Basilar length	59.1	59.1	61.1	57.2
Length of nasals (10 skulls)	25.2	25.1	27.3	23.0
Width of nasals	12.3	12.4	13.3	11.5
Length of audital tube (10 skulls)	18.9	18.5	21.0	16.0
Length of incisive foramen	6.6	7.2	8.7	5.7
Zygomatic width	55.5	54.5	59.6	49.5
Mastoid width of cranium	53.3	53.2	59.0	47.4
Alveolar length superior cheek teeth	18.8	19.0	19.9	18.2
Distance between infraorbital formamina	16.6	16.4	17.8	15.0
Mandible, transversely across angular process	23.1	22.4	25.0	19.9
Mandible, greatest length (12 skulls)	46.2	46.0	48.7	43.3

External Measurements of *Aplodontia rufa rufa*, From Vida and Vicinity of McKenzie Bridge, Oregon

	Average	Mean	Maximum	Minimum
Total length (9 skins)	345	348	387	310
Hind foot (7 skins)	56	56	59	54

Cranial Measurements of *Aplodontia rufa rufa* (12 Skulls), From the Vicinity of Seattle and Mount Baker Range, Washington, and the Chilliwack-Sumas District, British Columbia

	Average	Mean	Maximum	Minimum
Basilar length	59.6	59.5	62.1	57.0
Length of nasals (10 skulls)	26.1	25.2	27.2	23.2
Width of nasals	11.7	11.5	12.8	10.2
Length of incisive foramen	7.2	7.1	8.1	6.2
Zygomatic width	55.5	54.1	58.9	49.3
Greatest width of interpterygoid fossa	5.0	5.0	5.8	4.2
Mastoid width of cranium	52.2	52.5	55.7	49.4
Alveolar length of superior cheek teeth	19.1	19.1	20.0	18.3
Distance between infraorbital foramina	16.6	16.4	17.6	15.2
Mandible, transversely across angular process	22.6	23.0	25.9	20.2
Mandible, greatest length	47.6	47.3	49.5	45.1

External Measurements of *Aplodontia rufa rufa* (9 Skins), From the Vicinity of Seattle, Washington, and Chilliwack, British Columbia

	Average	Mean	Maximum	Minimum
Total length	331	332	345	318
Hind foot	56	56	58	54

Cranial Measurements of *Aplodontia rufa rufa* (7 Skulls), From Trinity and Siskiyou Counties, California

	Average	Mean	Maximum	Minimum
Basilar length	59.3	59.8	61.8	57.9
Length of nasals (6 skulls)	24.7	24.5	26.2	22.9
Width of nasals	11.7	11.8	13.0	10.7
Length of audital tube	19.1	19.4	21.1	17.7
Length of incisive foramen	7.2	7.2	7.6	6.7
Zygomatic width	56.1	55.9	60.4	51.4
Greatest width of interpterygoid fossa	5.1	5.1	5.3	4.8
Mastoid width of cranium	53.6	54.3	58.2	50.4
Alveolar length superior cheek teeth	18.8	18.7	19.2	18.2
Distance between infraorbital foramina	16.5	16.3	18.2	14.4
Mandible, transversely across angular process	24.0	23.9	26.0	21.7
Mandible, greatest length	48.3	47.7	51.3	44.5

External Measurements of *Aplodontia rufa rufa* (7 Skulls), From Trinity and Siskiyou Counties, California

	Average	Mean	Maximum	Minimum
Total length	340	340	370	310
Hind foot	59	58	63	53

Averages of External Measurements: Four specimens from Easton, Washington: total length, 354 mm. (345–368); hind foot, 59 (58–63). Eighteen specimens from Siskiyou, Oregon: total length, 332 (310–394); hind foot, 58 (52–63). Ten additional examples from the Siskiyou Mountains, California: total length, 349 (320–370); hind foot, 55 (53–58). Two specimens from Ashland Peak, Oregon: total length, 340, 352; hind foot, 60, 63. Two examples from Anna Creek, Mount Mazama: total length, 360, 385; hind foot, 58, 61. Three specimens from Fort Klamath, Anna Creek Canyon: total length, 333, 338, 370; hind foot, 54, 60, 57. Three specimens from Canyon Creek, California: total length, 345, 360, 370; hind foot, 60, 60, 60.

Remarks.—*Aplodontia rufa rufa* is a variable form embracing a number of local forms, some of which, if their extremes only were considered, would certainly rank as good subspecies. The number of these local variants (which have been noted from the Chilliwack-Sumas district, British Columbia; vicinity of Seattle, Puget Sound, Washington; Ashland Peak, Siskiyou and Fort Klamath, Oregon; the Siskiyou Mountains and Canyon Creek, California; and elsewhere), coupled with the great range of individual variation observable in series from the same general locality, make impracticable the recognition of subspecies within the range of *A. r. rufa* as here outlined.

Specimens of *rufa* from the immediate vicinity of Seattle, Washington, tend to have narrower nasals and rostra, mastoid width less, audital tubes of smaller caliber, and fossae set off anteriorly by lambdoidal ridge shallower than in typical material from Marmot, Oregon.

Externally they give a mass effect of grayish rather than brownish as in the Marmot examples. The differences are slight, however, and are not shown to the same extent by examples from nearby localities, as Mount Vernon, Hamilton, Sauk and Easton, in Washington, and the Chilliwack-Sumas district in British Columbia. The form from the vicinity of Seattle was recently described by the writer under the name *Aplodontia rufa grisea* (Taylor, 1916c, p. 497), but the examination of considerable additional material indicates the propriety of synonymizing *grisea* under *rufa*.

The effects of varying degrees of local isolation seem to be shown by specimens of *Aplodontia rufa* from the rough and mountainous region embraced in its range in southern Oregon and northern California. Groups of specimens from particular localities, however, do not show the constant differences which would be necessary to entitle them to recognition as subspecies. Examples of *rufa* from the Siskiyou-Trinity region of northern California (recently described by Kellogg, 1914, p. 295, as *Aplodontia chrysocola*) tend to have the caliber of the audital tube less than in typical *rufa*, the outline of the external auditory meatus a little flatter, the nasals slightly narrower and shorter, and coloration and quality of pelage slightly different. These tendencies, however, are overshadowed by the magnitude of the individual variation in the series. There appear to be several other local races of *rufa* as well entitled to subspecific recognition as *chrysocola*, but if they were to be described, no logical ranges could be given, and the degree of overlapping would make identification of specimens difficult if not impossible.

Intergradation between *Aplodontia rufa rufa* and neighboring subspecies is hinted at or directly demonstrated by specimens examined as follows: Intergradation with *columbiana*, by specimens from Sumas and Chilliwack, British Columbia; with *rainieri*, by examples from Easton, Washington; with *olympica*, by an example from Steilacoom, Washington; with *pacifica*, by specimens from Lane County, Oregon, and from Siskiyou, Oregon; with *californica*, by examples from Mount Mazama, Oregon, and Canyon Creek, California; and with *humboldtiana* by specimens from the divide between the Trinity and Klamath rivers, twelve miles north of Hoopa Post Office, northern California.

A considerable series of specimens from Siskiyou, Oregon, is puzzling, being *pacifica*-like in coloration, but larger, and in certain cranial characters more like *rufa*. As in other series, the range of

individual variation is great. Two examples from Siskiyou (nos. 56737, 56738, Biol. Surv. Coll.) are larger than the others of the series and have conspicuously heavier crania. Examples of *rufa* from Ashland Peak, also, are above the average in size, and show a likeness to *rainieri* in certain skull characters.

Intergradation between *rufa* and *californica* is best shown by several examples from Canyon Creek, California. These specimens combine the coloration and shortness of the rostrum of *rufa* with the squarer zygomatic arches and, in one case, the distinctive nasal outline of *californica*.

The distribution of aplodontias in northwestern California will bear additional intensive research. Specimens from the Trinity Mountains, east of Hoopa, are nearly typical of *rufa* from farther inland, although they show a slight tendency cranially in the direction of *humboldtiana*. Real intergradation is indicated, however, by three specimens from the divide between the Klamath and Trinity rivers, twelve miles north of Hoopa Post Office. Of these, an adult female (no. 98745, Biol. Surv. Coll.) both in cranial and external characters resembles *humboldtiana;* one young animal also (no. 97291, Biol. Surv. Coll.) resembles *humboldtiana;* while the third (no. 97290, Biol. Surv. Coll.), also a young animal, is nearest *rufa*. Examples referred to *rufa* have been taken in Hoopa Valley, as well as at Rio Dell, Humboldt County, California.

A tendency toward pattern formation is noted in specimens from Sauk, Washington. Extensive irregular patches of white beneath are conspicuous in several examples.

Aplodontia rufa olympica Merriam

Olympic Aplodontia

Aplodontia olympica Merriam (1899), p. 20.
Haplodontia olympica, Elliot (1899), pp. 251–253.

Type.—Male, young adult, no. 89549, U. S. Nat. Mus., Biol. Surv. Coll.; Quiniault Lake, Olympic Mountains, Washington; July 24, 1897; collected by R. T. Young; orig. no. 309; stuffed skin, with skull and jaws, all in good condition.

Specimens Examined.—Total number 29, from the following localities:

Washington: Pierce County—Fort Steilacoom, 1; Steilacoom, 1 (skull only). Clallam County—Happy Lake, Olympic Mts., 6; Olympic Mts., near head of Soleduc River (alt. 4500 ft.), 1; Port Angeles, 3. Jefferson County—Olympic Mts., head of north fork of Skokomish River, 2. Chehalis County—Quiniault Lake, 8. Mason County—Lake Cushman, 5; "Mason County," 2 (odd skulls).

Geographic Range.—Northwestern Washington, vicinity of Olympic Mountains, intergrading with *Aplodontia rufa rufa* in the vicinity of Steilacoom, southern Puget Sound.

Cranial Characters.—Skull moderate in size (see measurements below); nasals tending to be somewhat variable in outline; temporal lines or ridges tending to be more closely approximated anteriorly than in *rufa;* zygomatic arches tending to be lighter in weight than in *rufa;* thirteen out of seventeen crania examined with prominent postorbital process on the jugals, a character not developed to the same degree in any other form of *Aplodontia;* audital tubes tending to be of smaller caliber than in typical *rufa;* notch on upper side of external auditory meatus smaller and narrower than in typical *rufa.*

External Characters.—Above, in summer specimens, pinkish cinnamon to light ochraceous-buff, often with something of a grayish cast; the whole grizzled with more or less of an admixture of black hairs; head and face brownish or grayish; under parts grayish with a faint wash of pinkish buff or cinnamon buff.

Sexual Differences.—No appreciable external differences due to sex have been observed except in respect to the spot markings of the mammae and possibly a slight pallor ventrally in females.

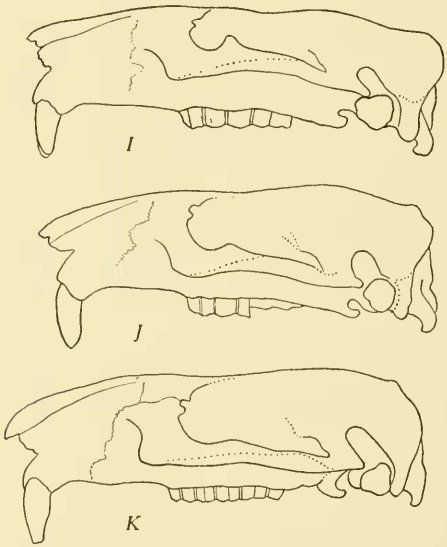
Cranial Measurements of *Aplodontia rufa olympica* (17 Skulls)

	Average	Mean	Maximum	Minimum
Basilar length	59.3	60.2	63.0	57.4
Length of nasals (12 skulls)	26.4	26.9	28.9	24.9
Width of nasals	11.9	12.1	13.3	10.8
Length of audital tube (12 skulls)	18.9	19.1	20.0	18.1
Length of incisive foramen	7.0	7.2	8.0	6.4
Zygomatic width (15 skulls)	54.6	54.9	56.9	52.8
Greatest width of interpterygoid fossa (12 skulls)	5.2	5.2	6.0	4.4
Mastoid width of cranium (16 skulls)	53.0	52.8	55.9	49.7
Alveolar length of superior cheek teeth	19.3	19.4	20.2	18.5
Distance between infraorbital foramina	16.5	16.4	17.5	15.3
Mandible, transversely across angular process	23.3	23.5	25.2	21.9
Mandible, greatest length	47.1	46.8	49.7	43.8

External Measurements of *Aplodontia rufa olympica* (10 Skins)

	Average	Mean	Maximum	Minimum
Total length	355	353	367	340
Hind foot	49	47	59	36

Molt and Seasonal Change.—The only months represented by available specimens of *olympica* are July and August. In the series at hand the molt begins about the middle of July, and is not completed till September at the earliest. One example (no. 67615, ♀, U. S. Nat. Mus., Biol. Surv. Coll.), secured August 17, is exceptional in that even at that late date it shows no sign of molt. On the basis of specimens at hand the winter coat is a little browner than the summer pelage.



Figs. I–K. Side view of crania of *Aplodontia rufa olympica*, to illustrate variation in development of postorbital process of the jugal. × 1. Fig. I, no. 66229, Biol. Surv. Coll.; fig. J, no. 6314, Field Mus. Nat. Hist.; fig. K, no. 89549, Biol. Surv. Coll.

Remarks.—*Aplodontia rufa olympica* is a feebly marked race of the *rufa* series occurring in the Olympic Mountain district of Washington, and grading insensibly into *rufa* to the east and southeast. Additional material from scattered localities in western and northwestern Washington may demonstrate so great a degree of variability as to make inadvisable the separate recognition of the Olympic Mountain form. The postorbital process on the jugal, the most important

character of the subspecies, is subject to considerable variation (text figs. I, J, K), and is more apparent in specimens from Lake Cushman than in those from Quiniault Lake. Specimens from Steilacoom (no. 2476, U. S. Nat. Mus., skull only) and Fort Steilacoom (no. 278, U. S. Nat. Mus., part of skull inside skin), here referred to *olympica*, might be referred to *rufa* with equal propriety.

Aplodontia rufa columbiana Taylor

Northern Aplodontia

Aplodontia californica columbiana Taylor (1916*c*), pp. 499–501.

Type.—Male adult; no. 1899, Coll. E. A. and O. Bangs, Mus. Comp. Zool.; Roab's Ranch, Hope, British Columbia; June 14, 1894; collected by W. C. Colt; stuffed skin with skull and jaws in good condition, except skin of foreleg injured in trap, and skull with left audital tube, region of foramen magnum, and hamulars, somewhat injured.

Geographic Range.—Vicinity of Hope, British Columbia, south in the Cascade Mountains of Washington; probably intergrading with *Aplodontia rufa rainieri* between the international boundary and Mount Rainier.

Specimens Examined.—Total number 11, from the following localities:

British Columbia: Yale Provincial District—Lake House, near Hope, 4; Roab's Ranch, Hope, 5. Washington: Skagit County—Head of Cascade River, 2.

Cranial Characters.—Skull heavy and large (see measurements below); for example, on basis of tables of measurements, furnishing maximum for the genus in length of nasals, zygomatic width, mastoid width, and greatest length of mandible; averages of length of nasals and zygomatic width exceeding the maximum in any other form; zygomatic arches moderate and, looking down upon them from above, transversely expanded posteriorly; temporal lines or ridges tending to be closely approaching, though never forming a distinct sagittal crest; dorsal outline of skull comparatively straight; audital tubes small calibered, dorso-ventral diameter tending to exceed anteroposterior diameter, tube thus appearing as if pinched anteroposteriorly.

External Characters.—Above, in summer skins, near light pinkish cinnamon, in some specimens as pale as light ochraceous-buff, in others as dark as pinkish cinnamon, grizzled with many blackish and sometimes a few whitish-tipped hairs; number and degree of concentration of black hairs on back variable; underparts showing faint brown wash,

sometimes nearer light pinkish cinnamon, sometimes nearer pinkish buff; general undertone of coloration ventrally pale drab-gray, with an insprinkling of varying numbers of blackish, whitish, cinnamon or buffy hairs; irregular areas of hair white from base to tip appearing in most of the males ventrally.

Sexual Differences.—The conspicuous white patches ventrally appear in males only, all the examples of that sex showing them to a greater or less extent. The spot marks about the mammae in May and July females are less conspicuous than usual. Of two females taken in July, one (no. 1894, Mus. Comp. Zool.) has the hair about the mammae practically worn off, while the other (no. 1895, Mus. Comp. Zool.) has the hair in the same region unworn. It seems likely that the condition of the hair about the mammae may be taken as an index to breeding activity.

Cranial Measurements of *Aplodontia rufa columbiana* (9 Skulls)

	Average	Mean	Maximum	Minimum
Length of nasals (7 skulls)	29.3	29.5	30.9	28.2
Width of nasals	12.8	12.9	13.8	12.0
Length of incisive foramen	8.0	7.8	8.5	7.2
Zygomatic width	62.3	60.9	64.0	57.9
Mastoid width of cranium	57.5	57.2	61.2	53.2
Alveolar length superior cheek teeth	19.3	19.3	19.8	18.8
Distance between infraorbital foramina	16.9	17.2	18.3	16.2
Mandible, transversely across angular process	24.6	24.5	26.1	23.0
Mandible, greatest length	51.2	51.9	54.9	48.9

External Measurements of *Aplodontia rufa columbiana* (9 Skins)

	Average	Mean	Maximum	Minimum
Total length	427	425	470	380

Remarks.—Available material indicates intergradation between *Aplodontia rufa columbiana* and *A. r. rufa* on the one hand and *A. r. rainieri* on the other. Specimens in the United States National Museum from the head of the Cascade River, Washington (nos. $\frac{30739}{42639}$, $\frac{30890}{42790}$, Biol. Surv. Coll.) are intermediate between *columbiana* and *rainieri*, although perhaps a trifle closer to the former. If, as seems likely, the distribution of *Aplodontia* is more or less continuous between Mount Rainier and the mountains in the Hope District, British Columbia, it is probable that one grades into the other by insensible degrees. Aside from its greater dimensions *columbiana* may be separated from *rufa* through its smaller-calibered, more pinched-up audital tubes, as compared with the larger, rounder tubes of *rufa*. *Columbiana* also has the zygomatic arch more expanded posteriorly than in *rufa*, as well as broader nasals posteriorly, and more closely approximated temporal

ridges. From *rainieri* typical *columbiana* differs in having cranial measurements averaging greater, the difference being shown in length and width of nasals, length of incisive foramina, zygomatic width, mastoid width, and greatest length of mandible. The external auditory meatus tends to be of different shape in *columbiana*, being pinched up anteroposteriorly, while in *rainieri* the meatus is rounder and tends to be flattened dorsoventrally.

Aplodontia rufa rainieri Merriam

Mount Rainier Aplodontia

Aplodontia major rainieri Merriam (1899*a*), p. 21.
Haplodontia rufa rainieri, Elliot (1901), p. 112.
A[*plodontia*]. *r*[*ufa*]. *rainieri*, Trouessart (1904), p. 348.

Type.—Male adult, skull and skin; no. 90144, U. S. Nat. Mus., Biol. Surv. Coll.; Paradise Creek, south side of Mt. Rainier, Washington, alt. 5200 ft.; Aug. 6, 1897; collected by Vernon Bailey; orig. no. 6122.

Specimens Examined.—Total number 9, all from Washington; Pierce County—Mt. Rainier, Paradise Creek, 9 (1 skull only).

Geographic Range.—Known only from vicinity of type locality.

Cranial Characters.—Skull large (see measurements below); nasals long and comparatively straight sided; posterior two-thirds of outline tending to be slightly convex laterally, but usually with a slight lateral embayment far back; rostrum broad, as in *columbiana;* zygomatic arches moderate, proportionally lighter in weight, not so much expanded near posterior root as in *columbiana*, flat beneath in vicinity of posterior root; temporal ridges tending to remain separated for their entire length by several millimeters; caliber of audital tubes small; external auditory meatus round or flattened dorsoventrally.

External Characters.—Above, in summer skins, light ochraceous-buff, grizzled with blackish, the black hairs often with silvery white tips; a tendency observable toward concentration of blackish on middle line of back; sides having comparatively few black hairs; underparts deep quaker drab to light quaker drab, marked with whitish generally, such markings more conspicuous anteriorly on the throat; spot marks near light brownish drab; a sparse insprinkling of blackish hairs; a faint wash of pinkish buff in some examples.

Age Variation.—There is not so striking an actual decrease in width of interorbital constriction with age as is usual in the genus.

The youngest specimens all have this measurement broad. In some of the older ones it is broad, in others narrow. The zygomata are usually squarer and more expanded in the adults than in the young. The mastoid process is exceeded by the audital tube in all the adults, being, however, only slightly exceeded in the oldest ones, while in young specimens the audital tube materially exceeds the mastoid process. The width of the palate between the third premolar and the incisive foramina remains about the same, or even increases slightly, with age. Looking at the crania in side view, the ventral outline of the rostrum is nearly plane in the young, with slight eminences observable at the posterior end of the incisive foramina. In the adults the outline tends to be more rounded, the slight eminences having disappeared.

Molt.—Specimens collected on Mount Rainier on August 6 and 7 are with one exception (no. 90143, ♀, U. S. Nat. Mus., Biol. Surv. Coll.) beginning to molt. In one example (no. 90145, ♀, U. S. Nat. Mus., Biol. Surv. Coll.) hair renewal is taking place on small areas on the sides; in another (no. 90144, ♂) new hair is coming in on the right side only on an area one inch wide and four inches long, as well as in an irregular area on the top of the head; still another (no. 90137, ♂) is molting extensively laterally as well as in a small area on the head. The condition of this specimen suggests that the molt begins on the sides, and sometimes becomes quite extensive before the head molt starts at all.

Cranial Measurements of Type and Topotypes of *Aplodontia rufa rainieri*

(4 Skulls)

	Average	Mean	Maximum	Minimum
Basilar length	62.1	63.6	65.4	61.9
Length of nasals (3 skulls)	27.4	27.4	27.7	27.1
Width of nasals	12.4	12.7	14.0	11.4
Length of audital tube (2 skulls)	19.1	19.1	19.9	18.4
Length of incisive foramen	7.7	7.7	8.2	7.2
Zygomatic width	59.5	58.6	62.0	55.3
Greatest width of interpterygoid fossa	5.6	5.6	5.9	5.4
Mastoid width of cranium	55.6	55.6	57.8	53.5
Alveolar length superior cheek teeth	20.0	19.9	21.0	18.9
Distance between infraorbital foramina	17.1	17.1	18.1	16.2
Mandible, transversely across angular process	25.7	26.0	28.2	23.9
Mandible, greatest length	50.8	50.8	52.9	48.8

External Measurements of Type and Topotypes of *Aplodontia rufa rainieri*

(4 Skins)

	Average	Mean	Maximum	Minimum
Total length	377	379	384	365
Hind foot	62	63	65	62

Remarks.—Comparisons of examples of *Aplodontia rufa rainieri* from the type locality and *A. r. columbiana* from the head of the Cascade River, Washington, with specimens of *A. r. rufa* from the Puget Sound district (Kirkland, Seattle, Chilliwack, Sumas), and then with examples from localities more or less intermediate geographically and altitudinally, as Sauk and Easton, Washington, demonstrate beyond a doubt that intergradation takes place between *A. r. rufa* and the *rainieri-columbiana* series. A gradual change is indicated from the lowland *rufa* type to the mountain *rainieri-columbiana* type in size, in general cranial characters, and, particularly, in the dimensions and outline of the nasal bones and the size and outline of the external auditory meatus. More abundant material would doubtless supply more complete evidence for intergradation.

A. r. rainieri tends to be grayer than *A. r. rufa*, decidedly grayer than in the typical form, and to have less brown beneath. The nasals in *rainieri* tend to be broader posteriorly, and the caliber of the andital tubes tends to be less.

Aplodontia rufa pacifica Merriam

Pacific Aplodontia

Aplodontia pacifica Merriam (1899*a*), p. 19.
Haplodontia pacifica, Elliot (1901), p. 114.

Type.—Female adult, skull and skin; no. 77372, U. S. Nat. Mus., Biol. Surv. Coll.; Newport, mouth of Yaquina Bay, Oregon; March 20, 1896; collected by B. J. Bretherton; orig. no. 2219.

Specimens Examined.—A total of 46, from the following localities:

Oregon: Clatsop County—Astoria, 2; Mishawaka, 1 (skin only). Tillamook County—Wilson River, McNamer's Camp, 1. Lincoln County—Newport, 8. Lane County—Florence, 7; Mercer, 3; Eugene, 1; Spencer Butte, 4; Seaton, 3; Mapleton, 3. Douglas County—Smith River, 2; Gardiner, 4. Coos County—Coquille, 3 (1 skull only); "Coos County," 1. Curry County—Agness, 1; Port Orford, 1 (skull only). Josephine County—Briggs Creek (alt. 3000 ft.), 13 miles southwest of Galice, 1.

Geographic Range.—Coast of Oregon, from Astoria on the north at least to Port Orford on the south; ranging inland locally, as in the vicinity of Eugene, Oregon, and gradually intergrading with *Aplodontia rufa rufa*, probably in a broad belt centrally on the Pacific slope of Oregon from the northern to the southern boundaries of the state.

Cranial Characters.—Skull comparatively small (see measurements beyond); nasals broad anteriorly, becoming only a little narrower posteriorly, fairly uniform in outline through the series, comparatively straight laterally, with little or no anterior dilation; temporal lines or ridges not strongly marked, never approximated, though sometimes approaching to within a few millimeters of one another anteriorly; zygomatic arches comparatively light in weight, with weakly developed postorbital processes in certain specimens; fossae in front of lambdoidal ridge shallow; audital tubes of small caliber, notch dorsally in tubes short and broad; averaging smaller, on the basis of specimens measured, than *Aplodontia rufa rufa*, *A. r. olympica*, or *A. r. humboldtiana* in basilar length, width of nasals, length of audital tube, zygomatic width, mastoid width, alveolar length superior cheek teeth, distance between infraorbital foramina, and greatest length of mandible.

External Characters.—Above, in winter specimens, sayal brown or cinnamon to pinkish cinnamon, in one specimen (no. 9077, Field Mns. Nat. Hist.) approximating pinkish buff; many glossy black hairs interspersed, especially on back; top of head usually conspicuously black; in most specimens a black area or ill-defined broad band starting at nose and continuing back over head and posteriorly along middle of back to posterior end of body, this indefinite band grading into the browner coloration of the sides; face grayish in most examples; underparts grayish, with a more or less distinct brown wash varying from cinnamon or pinkish cinnamon to warm buff or pinkish buff.

Cranial Measurements of *Aplodontia rufa pacifica* (23 Skulls)

	Average	Mean	Maximum	Minimum
Basilar length	57.0	57.5	62.1	52.9
Length of nasals (19 skulls)	24.8	23.9	26.5	21.4
Width of nasals	10.4	10.5	11.4	9.6
Length of audital tube (15 skulls)	16.8	16.8	17.9	15.7
Length of incisive foramen	6.6	6.6	7.7	5.5
Zygomatic width	51.5	51.6	56.1	47.1
Greatest width of interpterygoid fossa	4.6	4.4	5.3	3.5
Mastoid width of cranium (22 skulls)	49.1	50.0	52.9	47.2
Alveolar length superior cheek teeth	18.6	18.6	20.3	16.9
Distance between infraorbital foramina	16.0	15.8	17.5	14.1
Mandible, transversely across angular process	22.5	23.1	25.3	20.9
Greatest length of mandible (22 skulls)	45.7	45.6	49.4	41.9

External Measurements of *Aplodontia rufa pacifica* (23 Skins)

	Average	Mean	Maximum	Minimum
Total length	316	324	356	293
Hind foot	51	52	57	48

Molt.—The molting process is just beginning in specimens of this subspecies taken June 19, June 29, July 17, and September 12. The example taken on the date last named is exceptional in molting so late. The end of the molt is shown by specimens secured on October 6 and October 24. Others taken October 5, 9, and 24 have completely assumed the new pelage.

Remarks.—*Aplodontia rufa pacifica* is usually separable from *A. r. olympica* by both external and cranial characters. Cranially the absence in *pacifica* of the postorbital process on the jugal in most cases serves to distinguish it from *olympica*. The nasals tend to be narrower as well as shorter in *pacifica*, and to be straighter sided. The skull is usually smaller in *pacifica*, and the temporal lines are more accentuated. *Pacifica* is grayer headed than is *olympica*, and there is in *pacifica* a concentration of blackish on the middle line of the back which is not so apparent in *olympica*. There is more brownish dorsally in *pacifica*. Ventrally *pacifica* has a conspicuous brown wash, while in *olympica* the ventral brownness is less noticeable.

From *Aplodontia rufa rufa*, *A. r. pacifica* may usually be separated through having a greater concentration of blackish dorsally. A uniform brownish tone dorsally is never observed in typical *pacifica*, but in *rufa* it is often observed. In specimens which are not so distinctly brownish *pacifica* tends to be blackish while *rufa* tends to be grayish. Color fails completely to allocate certain specimens from intermediate localities. Thus examples from Siskiyou, Oregon, are in coloration *pacifica*, while in size and certain skull characters they are closer to *rufa*. Others from the vicinity of Eugene and other localities in Lane County, Oregon, have the coloration of *rufa* but certain other characters of *pacifica*. Cranially *pacifica* is usually separable from *rufa* through possession of nasals narrower anteriorly and proportionally broader posteriorly, lighter zygomatic arches, smaller average measurements throughout, audital tubes shorter and of lesser caliber, and shallower fossae anterior of the lambdoidal crests.

Smaller size and different coloration separate *Aplodontia rufa pacifica* from *A. r. humboldtiana*. From *A. r. pacifica* one gets the impression of rich brown with black hairs plentifully insprinkled and specially emphasized on the middle line of the back, while from *humboldtiana* one receives the impression of black sparsely interspersed with buffy. Cranially *pacifica*, while very close to *humboldtiana*, can usually be separated therefrom through the possession of nasals with straighter lateral outline.

Specimens of *Aplodontia rufa pacifica* from Mercer, Lane County, Oregon, tend to be uniformly larger than others from the coastal region. One of them (no. 1600, Univ. Ore. Mus.) gives the maximum measurement in a series of more than twenty skulls in basilar length, length of nasals, zygomatic width, alveolar length superior cheek teeth, distance between infraorbital foramina, distance transversely across angular process of mandible, and greatest length of mandible.

All specimens of aplodontia collected on or very close to the coast line (except the examples from Mercer just mentioned, and a skull only, from Port Orford, Oregon, no. 206368, U. S. Nat. Mus., Biol. Surv. Coll., which has broader nasals) are typical of the Newport form; but as specimens from points farther away from the coast are examined an increase in size is apparent, and the characters and coloration tend in the direction of *rufa*. To this category belong specimens from Lane County, referred to *pacifica* (as no. 204887, U. S. Nat. Mus., Biol. Surv. Coll.), examples from Siskiyou, Oregon, referred to *rufa* (see p. 460), and a specimen from Briggs Creek, Oregon, thirteen miles southwest of Galice (no. 205239, U. S. Nat. Mus., Biol. Surv. Coll.), referred to *pacifica*. Examples from these localities partake of the characteristics of two subspecies often in nearly the same degree, and some or all of them might be referred to one with almost as much propriety as to the other.

Intergradation with *rufa* is demonstrated by specimens of *pacifica* from Spencer Butte, seven miles south of Eugene, Oregon, and by examples of *rufa* from Siskiyou, Oregon. It seems probable that intergradation between the two forms takes place over a broad area north and south through central Oregon.

Aplodontia rufa humboldtiana Taylor

Humboldt Aplodontia

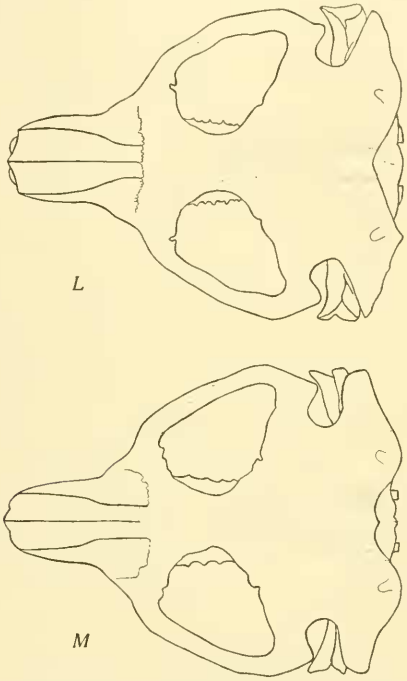
Aplodontia rufus (part), Price (1894), p. 328.
Haplodontia phaea (part), Elliot (1903), pp. 184, 185.
Aplodontia phaea (part), Stephens (1906), p. 95.
Aplodontia humboldtiana Taylor (1916*a*), pp. 21–23.

Type.—Male adult; no. 21162, Mus. Vert. Zool.; Carlotta, Humboldt County, California; January 4, 1914; collected by H. E. Wilder; orig. no. 1494; stuffed skin, with skull and jaws, all in good condition.

Specimens Examined.—A total of 24, from the following localities:

California: Del Norte County—Requa, 1. Humboldt County—Sam Lane's Ranch, 12 miles north of Hoopa, 3 miles southwest of Weitzpek, 3; Eureka, 5; Carlotta, 8; Cuddeback, 7.

Geographic Range.—The northern coast district of California from Humboldt Bay, Carlotta, and Cuddeback along the coast in Humboldt and Del Norte counties northward, at least to Requa; ranging inland locally in Humboldt County and intergrading with *A. r. rufa* in the vicinity of Weitzpek.



Figs. L, M. Dorsal view of crania of *Aplodontia rufa rufa* and *Aplodontia rufa humboldtiana*, to illustrate different nasal outline. × 1. Fig. L, no. 13326, Mus. Vert. Zool., *Aplodontia rufa rufa*, Jackson Lake, Siskiyou County, California; fig. M, no. 21162, Mus. Vert. Zool., *Aplodontia rufa humboldtiana*, Carlotta, Humboldt County, California.

Cranial Characters.—Skull moderate in size (see measurements below); nasal outline variable, but usually broad anteriorly, with a shallow embayment in lateral outline, not exceptionally compressed posteriorly (see text fig. M); zygomatic arches light to medium in

weight, with position of postorbital processes on the jugal faintly indicated in six crania out of sixteen; temporal ridges comparatively well marked, more accentuated than in either *Aplodontia rufa rufa* or *A. r. pacifica*, in some skulls widely separated, as in *pacifica*, in others approaching to within a few millimeters of each other, as in *rufa;* audital tubes tending to be of smaller caliber than in *rufa*, larger and straighter than in *pacifica;* incisive foramina comparatively short.

External Characters.—Above, light ochraceous-buff or pinkish buff, obscured by an admixture of black hairs which is nearly uniform over all upper parts—an insprinkling of silvery-tipped hairs augments the grizzled appearance—some specimens appearing conspicuously blackish; under parts near pale quaker drab with many silvery white hairs; the faintest possible wash of buffy brown observable in certain examples; a white spot usually present posteriorly in the vicinity of the external genitalia.

Sexual Differences.—Three males out of eleven have total length greater than the maximum of that measurement in the females; six have tail vertebrae longer than this maximum, and six also have hind foot longer. Comparison of fall examples demonstrates that the three darkest specimens are males, their darker coloration being more evident ventrally. In this species in fall pelage the spot marks about the mammae do not afford a distinctive character. While they are in evidence in certain specimens of both sexes, they are lacking in others. In examples having the spot marks, females have them more accentuated than males.

There is a tendency for the ridges and processes in the skulls of males to be somewhat more accentuated than in those of females. Temporal lines or ridges appear to come closer together with old age in males than in females.

Molt.—Two young specimens (nos. 9061, 9062, Field Mus. Nat. Hist.), collected August 16 and August 18, respectively, are molting into the adult pelage. The adult coat has replaced the juvenal pelage everywhere in these specimens except in a narrow band across the shoulders, although a patchy appearance posteriorly in one of them (no. 9061) suggests that the molt is incomplete in that region. An adult specimen (no. 21159, ♂, Mus. Vert. Zool.) taken at Carlotta, Humboldt County, November 5, has almost completely assumed the fresh pelage. New hair is still coming in on a narrow longitudinal line on the back posteriorly. Another specimen (no. 21156, ♂, Mus. Vert. Zool.) taken October 29 has the winter pelage complete.

CRANIAL MEASUREMENTS OF *Aplodontia humboldtiana* (15 SKULLS)

	Average	Mean	Maximum	Minimum
Basilar length	58.8	58.7	62.5	55.0
Length of nasals (11 skulls)	24.5	23.8	26.0	21.9
Width of nasals	11.2	11.2	12.4	10.0
Length of audital tube (12 skulls)	18.4	18.0	19.5	16.5
Length of incisive foramen	5.9	6.5	8.2	4.8
Zygomatic width	53.8	53.2	57.9	48.6
Greatest width of interpterygoid fossa	5.5	5.7	6.7	4.8
Mastoid width of cranium	52.3	51.7	57.4	46.0
Alveolar length superior cheek teeth	18.8	18.6	19.7	17.6
Distance between infraorbital foramina	16.4	17.1	18.9	15.4
Mandible, transversely across angular process	22.2	21.6	23.9	19.4
Mandible, greatest length	48.1	48.1	50.7	45.6

EXTERNAL MEASUREMENTS OF *Aplodontia humboldtiana* (15 SKINS)

	Average	Mean	Maximum	Minimum
Total length	346	333	367	300
Hind foot	56	56	63	50

Remarks.—*Aplodontia rufa humboldtiana* is larger and less richly colored than *Aplodontia rufa pacifica* of the coast region of Oregon (see p. 469). *Humboldtiana* is similar in coloration to *A. r. rufa*, of the Trinity-Siskiyou Mountain region to the eastward, but darker, a paler hue of the brown series of colors being interspersed with the black hairs. The Humboldt aplodontia is not so black as is *A. r. nigra*, its nearest neighbor on the south, although in certain cranial characters, notably width of nasals, length of incisive foramen, zygomatic width, greatest width of interpterygoid fossa, and mastoid width, it is closer to *nigra* than to any other one of its neighbors.

Specimens from Sam Lane's Ranch, twelve miles north of Hoopa and three miles southwest of Weitzpek, on the divide between the Klamath and Trinity rivers (nos. 97290, 97291, 98475, U. S. Nat. Mus., Biol. Surv. Coll.), here referred to *humboldtiana*, show intergradation in the direction of *A. r. rufa*.

Aplodontia rufa californica (Peters)

Sierra Aplodontia

Aplodontia leporina (part), Audubon and Bachman (1854), pp. 99–103.
Marmot, Mammoth Mole, Calif. Acad. Nat. Sci. (1855), p. 71.
H[aplodon]. leporinus var. *Californicus* Peters (1865), pp. 177–179.
H[aploodon]. californicus, Lilljeborg (1866), p. 41.
Haplodon rufus, Coues (1877*b*), p. 557.
Aplodontia major Merriam (1886), p. 316.
H[aplodon]. major, Townsend (1887), p. 174, footnote.
H[aplodontia]. major, Elliot (1899), p. 251.
Haplodontia rufa californica, Elliot (1901), p. 112.
Aplodontia rufa californica, Trouessart (1904), p. 348.
Aplodontia californica, Grinnell (1913), p. 344.

Type.—A skin and skull in the Berlin Museum.

Type Locality.—Assumed to be the Sierra Nevada of California (Grinnell, 1913, p. 344); specimens from Blue Cañon in the central Sierra may be regarded as typical.

The tenability of Peters' name for this subspecies depends on answers to two questions: first, was Peters' specimen an *Aplodontia* at all, and, second, if an *Aplodontia*, what was its source? Answering the first, it seems clear from Peters' description, which is fairly detailed, which takes account of both skull and skin, and which was evidently drawn up with Baird's figure of the skull of *Aplodontia leporina* at hand, that the mammal discussed is an aplodontia. The fact that Peters fell into error in a portion of his description does not appear to alter the case from the nomenclatural standpoint. *Aplodontia* is the only known mammal occurring in California or North America which possesses approximately the characters set down by Peters. His references to the inflected angle of the jaw of the animal he had in hand and to its short tail alone suffice to demonstrate its position.

The following considerations seem germane to a discussion of the second question: The discovery of gold in the Sierra Nevada of California in 1848 brought great numbers of people to this section from all parts of the world. It is well known that aplodontias occur in the Sierra not far from the center of early mining activity, and it is highly probable that some early naturalist collected here the specimen which later became the basis of Peters' new form.[1]

The type of "*H*[*aplodon*]. *leporinus* var. *Californicus*" is stated to have come "aus den Gebirgen Californiens." From early times the Sierra Nevada have impressed travelers and map makers as the most noteworthy mountains within the state. The only other mountains within its boundaries in which aplodontias occur are the Trinity-Siskiyou ranges of northern California. The chance that Peters' specimen came from these then little known mountains rather than from the Sierra Nevada is slight.

Absolute finality of decision as to the name of the Sierra aplodontia is impossible without access to Peters' specimen. In deference

[1] Soon after the discovery of gold California became comparatively well known, even in Europe. Phillips (*List of Maps of America in the Library of Congress*, 1901, pp. 183–186) lists no less than four maps published in Europe between 1848 and 1865 (the date of Peters' publication of the name *californica*), according to which the boundaries of the state are approximately correct. The maps are those of Duflot de Mofras, Paris, 1849; Desfontaines, Paris, 1849; Reimer, Berlin, 1856; and Rossi, Paris, 1863.

to the above considerations, however, the writer finds himself unable to agree with Dr. C. Hart Merriam in regarding Peters' name as untenable, but is forced to consider that the balance of the evidence now available favors its validity.

Specimens Examined.—A total of 75, from localities as follows:

California: Siskiyou County—Mt. Shasta, Upper Ash Creek (alt. 7000 ft.), 2; Mt. Shasta, Upper Mud Creek (alt. 7000 ft.), 8. Lassen County—Lassen Peak, upper edge Canadian zone, east side, 1; Susanville, mountains 12 miles west, 1. Sierra County—Salmon Lake (alt. 6600 ft.), 5. Placer County—Blue Cañon, 21. El Dorado County—Lake Tahoe, Emerald Bay, 3; South Fork of American River, 1. Alpine County—Hope Valley, 10. Mariposa County—Yosemite Park, East Fork Indian Cañon, 2; near Porcupine Flat, 1; head of Lyell Cañon (alt. 9700 ft.), 5; Mt. Lyell, 4; Chinquapin (alt. 6256 ft.), 5. Mono County—Mammoth, 4 (2 skulls only).

Geographic Range.—The Sierra Nevada of California, from Mt. Shasta on the north at least to Mammoth, Mono County, on the south. Zonal range, Boreal.

Cranial Characters.—Skull large (see measurements below), similar, in dimensions, to *Aplodontia rufa rainieri* and *A. r. columbiana*, averaging slightly larger than *A. r. rufa;* rostrum comparatively long, zygomatic arches heavy, tending to be squarer anteriorly than in any other aplodontia; zygomatic arches usually not so much expanded at the posterior root, viewing cranium on its dorsal or ventral aspect, as in *columbiana;* distinct fossa present in typical material on under surface of expanded portion near posterior root, unlike most examples of *rainieri* and *columbiana* in this respect; postorbital processes on the jugal sometimes faintly indicated; temporal ridges tending to approach to within a few millimeters of each other for their entire length, variously accentuated in different specimens; caliber of audital tubes variable, but averaging decidedly greater than in either typical *rainieri* or in *columbiana*, about the same as in *rufa;* external auditory meatus round or slightly flattened dorsoventrally, as in *rainieri*.

External Characters.—Above, in summer skins, pale ochraceous-buff to ochraceous-buff, in most specimens uniformly grizzled with blackish, and with an insprinkling of silvery tipped hairs; amount and concentration of black varying to a considerable extent; white spot at base of ear (pl. 29); underparts light mouse gray to quaker drab, with insprinkling of black hairs, often silvery tipped, certain specimens with indistinct wash of brown coloration near pinkish buff or light buff, others with a suggestion of light ochraceous-buff. Coloration of winter specimens only slightly different from that in summer.

While the coloration of adults and young is similar, the latter are woollier and grayer in general appearance than in the former.

Age Variation.—Cranially there is a tendency for the sutures between the nasals posteriorly, the premaxillaries and the frontals to remain open longer than is the case in other species. The interorbital constriction undergoes a proportional and with some exceptions an actual decrease with age. The zygomata are heavier in adults than in the young and tend to be more bowed outward, or squarer, anteriorly. Temporal lines or ridges come closer together with age. In some old adults of this species they almost coalesce anteriorly, while remaining only four or five millimeters apart posteriorly. Although the mastoid process tends to grow laterad more rapidly than the audital tube with age, in almost all the available specimens the latter exceeds the former in length.

Sexual Differences.—The crania of males tend to be larger than those of females in nearly all measurements; zygomata are heavier in males; and the temporal lines or ridges tend to be more accentuated and more closely approximated. The females tend to have interpterygoid fossa proportionally broader than the males. In seven out of eleven males measured the mandible, transversely across angular process, is greater than the maximum for the females. Examination of the material before me confirms C. Hart Merriam's (1886, pp. 327, 328) conclusions regarding cranial differences due to sex in this species except in certain details respecting the suture which separates the frontal bones from the premaxillaries and nasals, and in the outline of the postzygomatic notches. In Merriam's material the suture in question is open in the females and closed in males, while in the material before me there is nearly as strong a tendency toward effacement of the suture in females as in males. In Merriam's material the postzygomatic notches are larger in females, while in the material now available no constant sexual differences in this respect can be made out. Our specimens like those examined by Merriam have the skulls of the females less heavy and massive than those of the males, the occipital crest not so highly developed, and the zygomatic arches not so much bowed outward.

Molt and Seasonal Change.—As in other subspecies of *rufa*, molting takes place during late summer and early fall. The earliest molting specimen examined is a female taken July 21. Most examples taken during August and September are well along in the molting process, while those secured in October show its last stages, and a

specimen taken on October 15 (no. 192618, ♂, U. S. Nat. Mus., Merriam Coll.) has the winter pelage complete. An example taken on August 27 (no. 110241, ♂ ad., U. S. Nat. Mus., Biol. Surv. Coll.) shows no sign of molt, to all appearances having assumed the fresh pelage. One taken August 29 (no. 110243, ♀ ad., U. S. Nat. Mus., Biol. Surv. Coll.) has the new pelage nearly complete. A few scattered hairs are still coming in on the sides posteriorly and far back ventrally. These two specimens have completed the molt at an exceptionally early date. In one specimen (no. 67854, ♀, September 8, U. S. Nat. Mus., Biol. Surv. Coll.) the pelage has been renewed dorsally on the anterior three-fourths of the body. In another (no. 192617, ♂, October 12, U. S. Nat. Mus., Merriam Coll.) all the pelage dorsally has been renewed except in a band about two inches wide across the body just back of the shoulders.

Young specimens do not conform exactly to the schedule of the adults. In one example (no. 22617, Mus. Vert. Zool.) taken June 19 the new pelage covers the head and extends posteriorly to a line transversely across the body from one to two inches back of the ear; it appears in a small spot just back of the nape of the neck; and it is more conspicuous than elsewhere in a broad band about four inches wide, extending from side to side across the body in the middle of the back. Often a vigorous hair renewal becomes apparent only upon a close examination. A juvenal (no. 192615, ♂, October 9, U. S. Nat. Mus., Merriam Coll.) in which the hair is being renewed on hips, head, and neck exemplifies this state of affairs. In a third juvenal (no. 110247, August 30, U. S. Nat. Mus., Biol. Surv. Coll.) new hair is coming in on areas two inches wide and three inches long far back on the sides.

The fresh pelage is longer and a trifle browner than the worn pelage it replaces. Wear has a tendency to expose the darker under portions of the pelage, so that the summer pelage appears a little darker than the fresh fall pelage. The differences between the pelages are slight at most, and often none are observable.

Remarks.—*Aplodontia rufa californica* differs from *A. r. rufa* of the Trinity-Siskiyou region of southern Oregon and northern California in having more grayish coloration and in cranial characters as follows: Nasal outline uniform in *californica*, moderately broad in front, moderately narrow posteriorly (nasals in *rufa* variable, usually proportionally broader anteriorly and narrower posteriorly); widest portion of nasals usually most anterior point where nasals touch

maxillaries (often posterior of this point in *rufa*); shallow embayment in lateral outline of nasals posteriorly (variable in *rufa*); rostrum and nasals longer in *californica*, zygomatic arches squarer anteriorly, caliber of audital tubes averaging greater (about equal to caliber in typical *rufa*). From *A. r. rainieri*, *californica* differs in the following skull characters: nasals tending to be broadest at a more anterior point; a more pronounced tendency observable toward approximation of temporal ridges; heavier zygomatic arches, squarer anteriorly; and great caliber of audital tubes.

Cranial Measurements of *Aplodontia rufa californica* (14 Skulls)

	Average	Mean	Maximum	Minimum
Basilar length	61.1	62.4	65.1	59.6
Length of nasals (8 skulls)	26.8	26.9	28.4	25.4
Width of nasals	12.1	12.0	12.8	11.2
Length of audital tube (12 skulls)	19.1	18.9	20.5	17.2
Length of incisive foramen	7.6	7.6	8.2	7.1
Zygomatic width	57.6	57.0	60.9	53.1
Greatest width of interpterygoid fossa	5.2	5.2	5.8	4.7
Mastoid width of cranium	54.2	53.9	57.0	50.7
Alveolar length of superior cheek teeth	19.6	19.6	20.7	17.5
Distance between infraorbital foramina	17.6	17.4	18.4	16.4
Mandible, transversely across angular process	24.5	24.4	26.6	22.1
Mandible, greatest length	50.5	49.9	53.2	46.7

External Measurements of *Aplodontia rufa californica* (17 Skins)

	Average	Mean	Maximum	Minimum
Total length	352	352	380	325
Hind foot	60	59	64	55

Cranial measurements of three males from Blue Cañon, California: basilar length, 64.3, 63.1, 62.8; length of nasals, 29.1, 27.0, 27.0; width of nasals, 12.6, 13.0, 12.8; zygomatic width, 61.9, 61.4, 61.2; mastoid width, 59.4, 59.9, 57.9. Cranial measurements of three females from the same locality: basilar length, 60.7, 61.9, 60.5; length of nasals, 27.6, 27.2, 27.0; width of nasals, 12.0, 11.9, 12.2; zygomatic width, 55.5, 60.9, 57.8; mastoid width, 53.4, 57.9, 54.8.

Californica is one of the more consistent subspecies of *Aplodontia rufa*, maintaining its characters with considerable uniformity throughout its range. Still, a series of specimens from Mount Shasta, California, while indistinguishable cranially from typical *californica*, is characterized by slightly darker coloration dorsally.

Squareness anteriorly of the zygomatic arches and outline of the nasals in specimens of *rufa* from Mount Mazama in southern Oregon suggest intergradation with *californica*, as do also certain cranial characteristics of examples from Cañon Creek, California. The latter exemplify a tendency to combine the square zygomatic arches and the distinctive nasal outline of *californica* with the short rostrum and browner coloration of *rufa*.

Aplodontia rufa nigra Taylor

Point Arena Aplodontia

Aplodontia nigra Taylor (1914), pp. 297–300.

Type.—Male adult; no. 20320, Mus. Vert. Zool.; Point Arena, Mendocino County, California; July 10, 1913; collected by C. L. Camp; orig. no. 1003.

Specimens Examined.—Total number 4, all from California: Mendocino County—Point Arena.

Geographic Range.—Known only from the type locality, where it is found within an area of approximately twenty-four square miles.

Cranial Characters.—Skull moderate in size (see measurements below); nasals dilated anteriorly, comparatively contracted posteriorly; zygomatic arch medium in weight, squarish anteriorly; position of postorbital process faintly indicated; temporal lines or ridges not closely approaching; incisive foramina short; notch dorsally on external auditory meatus deeper than in *Aplodontia rufa humboldtiana*, more as in *A. r. pacifica*.

External Characters.—Summer specimens, above shiny black, with a sparse insprinkling of pinkish buff hairs and with plumbeous bases of the hairs showing through to a certain extent, the whole giving the impression of shiny black faintly sprinkled with grayish; sides paler than back, prevailingly pinkish buff, with heavy insprinkling of black hairs; head tending to be shiny black; face dark quaker drab; underparts cinereous to plumbeous, lightly washed with pinkish buff.

Age Variation.—This subspecies exhibits a remarkable similarity in the characters of adult and young. The coal black dorsal coloration, as well as the anterior dilation of the nasal outline, are conspicuous in both. In one young example (no. 20321, Mus. Vert. Zool.) a single small bony element is marked off by sutures in the interparietal region. The zygomata are decidedly heavier in the adult than in the young, as well as somewhat more expanded anteriorly.

Molt.—Three young at hand (nos. 20318, 20319, and 20321, Mus. Vert. Zool., taken July 9 to 11) are molting from the juvenal pelage into that of the adult. The new pelage is more intensely brown and black than the gray-black pelage of the juvenal, the brown being more emphasized laterally, the black dorsally.

Remarks.—*Aplodontia rufa nigra* is the most strikingly marked subspecies of mountain beaver known, its dorsal coloration rendering

it the darkest form as yet characterized. Both old and young may be separated with certainty on coloration alone from any known form of the genus. The anterior dilation of its nasal outline serves to separate it from *A. r. phaea* and *A. r. pacifica*. From *A. r. humboldtiana*, its nearest neighbor on the north, it is separated by its darker coloration and, in general, smaller size.

Cranial Measurements of *Aplodontia rufa nigra* (1 Cranium)

Basilar length	57.1
Length of nasals	23.2
Width of nasals	11.0
Length of audital tube	17.3
Length of incisive foramen	6.0
Zygomatic width	53.7
Greatest width of interpterygoid fossa	5.6
Mastoid width of cranium	51.8
Alveolar length superior cheek teeth	18.4
Distance between infraorbital foramina	15.3
Mandible, transversely across angular process	22.7
Mandible, greatest length	45.1

External Measurements of *Aplodontia rufa nigra* (1 Skin)

Total length	346
Hind foot	55

That *Aplodontia rufa nigra* finds in *A. r. humboldtiana* and in *A. r. phaea* its nearest relatives seems reasonably clear. The blackish coloration of the Point Arena form suggests the dark coloration of the Humboldt Bay race, while its size and the length of incisive foramina of the skull show that it is not far from *phaea*.

The distinctive coloration of all the known specimens of *A. r. nigra* and its geographical isolation constitute, perhaps, arguments for its recognition as a full species. On the other hand, the paucity of material representative of the form, coupled with the amplitude of individual variation in other forms in the genus, and with the evident overlapping of cranial characters with *humboldtiana* on the one side and *phaea* on the other, indicate the propriety, for the present at least, of allocating *nigra* as a subspecies of *rufa*.

Aplodontia rufa phaea Merriam

Point Reyes Aplodontia

?Haplodon rufus, True (1885), p. 596.
Aplodontia phaea Merriam (1899*a*), p. 20.
Haplodontia phaea, Elliot (1901), p. 114.

Type.—Male adult, skin and skull; no. 186475, U. S. Nat. Mus., Merriam Coll. (no. $\frac{2645}{3273}$); Point Reyes, Marin County, California; August 1, 1886; collected by C. A. Allen; orig. no. 142.

Specimens Examined.—A total of 36, from the following localities:

California: Marin County—Five miles west of Inverness, 9; six miles west of Inverness, 7; four miles south of Olema, 3; Lagunitas, 2; Point Reyes, 15 (1, skull only; 3, jaws only, labeled under one number).

Geographic Range.—Favorable situations in Marin County, California, where it is found within an area of approximately 110 square miles.

Cranial Characters.—Skull small (see measurements below); nasals not extreme, nearly straight sided, narrow across posterior ends, not extremely wide at anterior ends; zygomatic arch light, not conspicuously squarish anteriorly; temporal lines or ridges not unduly accentuated, wide apart; audital tube comparatively large calibered; fossae anterior of lambdoidal crests shallow; notch dorsally on external auditory meatus shallow; incisive foramina short; interpterygoid fossa narrow.

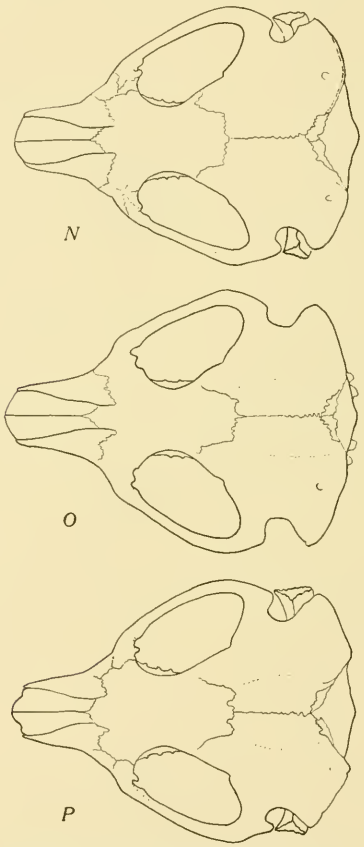
External Characters.—Above, in summer skins, pinkish cinnamon to cinnamon-buff, in winter approximating cinnamon or even tending toward sayal brown, sometimes grayish; all upperparts uniformly grizzled with black-tipped hairs, which are somewhat more numerous on the back than on the sides. Underparts French gray to plumbeous, with a sparse insprinkling of black hairs; the whole ventral surface washed with light ochraceous-buff to pinkish buff. Two specimens (nos. 192629, 192631, U. S. Nat. Mus., Merriam Coll.) have small white spots on the throat. One example (no. 192635, U. S. Nat. Mus., Merriam Coll.) is melanistic, being light seal brown in color above and below.

Age Variation.—Illustrative of the decrease in width of the interorbital constriction with age are the measurements obtained from ten specimens of this species, in which the ratio of the width of interorbital constriction to basilar length varies from 26.2 per cent in a very young example to only 17.1 per cent in an adult.

In several of the youngest specimens there are two small bones marked off by sutures in the interparietal region. They soon disappear through ankylosis.

In ventral view it may be noted that with age the part of the palate between the third premolar and the incisive foramina becomes narrower. One striking feature noticed here is that while the basilar length varies with age in certain specimens examined from 42.9 mm. to 55.5 mm., the width of the palate between right and left premolar four remains constant at about 5 millimeters.

The ratio of the width of the angular portion of the jaw to the length of the jaw undergoes, in specimens measured, a 5 per cent increase with age. In youth there is a smooth space between the inner prominence of the angle and the ridge in front of the masseteric fossa, while in old age there is a tendency for this ridge to be continued



Figs. N–P. Dorsal view of crania of young specimens of *Aplodontia rufa phaea*, to illustrate marking off of interparietal elements. × 1. Fig. N, no. 20302, Mus. Vert. Zool.; fig. O, no. 20308, Mus. Vert. Zool.; fig. P, no. 20316, Mus. Vert. Zool.

across the lower side of the ramus and connected with the inner prominence of the angle.

Seasonal Change.—Molt begins the last of July or the first of August. Specimens taken September 17 and November 9 have the process about completed, and one secured November 12 has entirely finished molting. More black hairs are sprinkled into the winter pelage, and the hair is somewhat longer and thicker. The spot marks about the mammae in the females are much less conspicuous in winter than in summer.

CRANIAL MEASUREMENTS OF *Aplodontia rufa phaea* (11 SKULLS)

	Average	Mean	Maximum	Minimum
Basilar length	55.6	54.8	58.6	51.1
Length of nasals (4 skulls)	21.5	22.0	23.7	20.3
Width of nasals	9.6	9.5	10.3	8.7
Length of audital tube (9 skulls)	16.3	16.4	17.2	15.6
Length of incisive foramen	6.2	6.1	7.6	4.5
Zygomatic width	50.3	49.5	53.0	46.0
Greatest width of interpterygoid fossa	4.3	4.2	4.7	3.8
Mastoid width of cranium	47.2	46.4	51.0	41.9
Alveolar length superior cheek teeth	18.4	18.5	19.2	17.9
Distance between infraorbital foramina	15.1	15.3	16.5	14.1
Mandible, transversely across angular process	21.6	21.7	22.8	20.7
Mandible, greatest length	43.1	43.4	45.1	41.7

EXTERNAL MEASUREMENTS OF *Aplodontia rufa phaea* (13 SKINS)

	Average	Mean	Maximum	Minimum
Total length	308	312	344	280
Hind foot	52	52	57	48

Remarks.—*Aplodontia rufa phaea* is the smallest subspecies in the genus. It is also the palest of the coastal forms of *Aplodontia* (*pacifica, humboldtiana, nigra, phaea*) occurring in Oregon and California. Cranially its closest affinities seem to be with *Aplodontia rufa nigra*.

In spite of the geographical isolation of the Marin County form, it is very similar, in general coloration, to some examples of *rufa;* nor are its cranial characters sufficiently distinctive to warrant its recognition as of more than subspecific rank.

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Cope, E. D.

1878. On some characters of the Miocene fauna of Oregon. Palae. Bull., 30, 1–16.
Original description of *Meniscomys hippodus*, new genus and species (pp. 5–6); and of *Meniscomys multiplicatus*, new species (p. 6).

1883. The extinct rodentia of North America. Amer. Nat., 17, 43–57, 13 figs. in text.
Haplodontiidae mentioned in comparisons with Castoridae and Sciuridae (p. 54); reference to *Haplodonta* [=*Haplodontia*] *rufa* (p. 55).

Coues, E.

1877*a*. The mountain boomer, or showtl. Amer. Nat., 11, p. 434.
Paragraph introductory to publication of letter from Dr. F. S. Matteson regarding habits of *Aplodontia leporina*.

1877*b*. "Haplodontidae" *in* Monographs of North American Rodentia, *in* Rep. U. S. Geol. Surv. Terr., **11**, no. 9, pp. 543–601, 1 pl.

Discussion of characters and relationships of family, genus and species, including remarks on history, relationships and habits; accompanied by one plate (pl. 6) illustrating dorsal, lateral and ventral view of skull (pp. 549–599).

1890. *Haplodon*. Century Dictionary (New York, Century), Part x, p. 2712.

Discussion of spelling of the generic name for *Aplodontia*.

Desmarest, M. A. G.

1822. Mammalogie, ou description des espèces de mammifères. (Paris, Agasse), pp. i–viii, 277–530. The whole = vol. 126 of the Encyclopédie methodique.

Unimportant fragmentary compilation of matter on "Anisonyx? rousse" (footnote, p. 330).

Douglas, D.

1836*a*. A sketch of a journey to the northwestern parts of the continent of North America, during the years 1824–1827, *in* Hooker, W. J., Companion to Botanical Magazine (London, Curtis), **2**, 83–140.

The *Ground Rat*, or *Arctomys* (*Arctomys brachyurus?*), mentioned as occurring on the Cowalidsk River (p. 101).

1836*b*. Accounnt of Mr. Douglas' second visit to the Columbia; his excursions in California; and his visit to Mouna Roa in the Sandwich Islands; with particulars respecting his death. *Ibid.*, **2**, 146–178.

Remarks on geographic limits of California (p. 149).

1914. Journal kept by David Douglas during his travels in North America, 1823–27 (London, Wesley), 364 pp., frontispiece.

Arctomys [= *Aplodontia*] mentioned (pp. 59, 156); ground rat (p. 156).

Elliot, D. G.

1899. Catalogue of mammals from the Olympic Mountains, Washington, with descriptions of new species. Field Columb. Mus. Zool., **1**, 241–276, pls. 41–61, several unnumbered figs. in text.

Treatment of *Haplodontia olympica*, with illustrations, and casual mention of *H. rufa* and *H. major* (pp. 251–253, pls. 41, 42).

1901. A synopsis of the mammals of North America and the adjacent seas. Field Columb. Mus. Zool., **2**, xiv+471, 49 pls., 94 figs. in text.

Haplodontidae characterized (p. 111); six forms of *Haplodontia* listed, as follows: *Haplodontia rufa; H. r. californica; H. r. rainieri; H. pacifica; H. phaea; H. olympica* (pp. 112–114).

1903. A list of mammals obtained by Edmund Heller, collector for the Museum, from the coast region of northern California and Oregon. Field Columb. Mus. Zool., **3**, 175–198.

References to *Haplodontia* (pp. 175, 179, 184, 185); *Haplodontia pacifica* (p. 184); *H. phaea* (pp. 184–185).

1905. A check list of mammals of the North American continent, the West Indies and the neighboring seas. Field Columb. Mus. Zool., **6**, v+761, frontispiece.

Genus *Haplodontia* listed (p. 126); six forms of *Haplodontia* enumerated, as follows: *Haplodontia rufa; H. r. californica; H. r. rainieri; H. pacifica; H. phaea; H. olympica* (pp. 126–128).

1907. A catalogue of the collection of mammals in the Field Columbian Museum. Field Columb. Mus. Zool., **8**, viii+694, 92 figs. in text.

Four forms of *Haplodontia* listed as being represented in the Museum Collection, as follows: *Haplodontia rufa; H. pacifica; H. phaea; H. olympica* (pp. 188–190).

Fischer, J. B.

1830. Synopsis mammalium. (Stuttgart, Cotta), xli + 752 pp.

Comments given on *Apludontia leporina;* of little importance (addenda, pp. 330, 398, 399, errors for 530, 598, 599).

Forsyth Major, C. J.

1893. On some Miocene squirrels, with remarks on the dentition and classification of the Sciurinae. Proc. Zool. Soc. London, **1893**, 179–215, pls. 8–11.

Refers to Winge's classification of rodents. Sciuridae and Anomaluridae derived from the Haplodontidae (p. 196, footnote).

Furlong, E. L.

1910. An aplodont rodent from the Tertiary of Nevada. Univ. Calif. Publ. Bull. Dept. Geol., **10**, 397–403, 6 figs. in text.

Original description of *Aplodontia alexandrae.*

Geoffroy Saint-Hilaire, I.

1826. La marmotte rousse, *Arctomys rufa.* Dict. Class. d'Hist. Nat. (Paris, Bandouin Frères), **10**, 1–642.

General compiled account of *Aplodontia,* headed as above; also discussion of old world and new world species referred to *Arctomys* (pp. 186–187).

Gerrard, E.

1862. Catalogue of the bones of mammalia in the collection of the British Museum (London, British Museum), iv+296 pp.

A skull of *Aplodontia leporina* from Chilakiveyak [= Chilliwack] River, British Columbia (p. 224), and another from the Wilkes Exploring Expedition (addenda, p. 296) are in the collection.

Gervais, P.

1854. Histoire naturalle des mammifères. (Paris, Curmer), xxiv + 420 pp., pls. 19, unnumbered figs. in text. The "Genre Aplodontie" referred to the "Tribu des Saccophoriens" of the "Famille des Pseudostomides"; associated with the genus *Saccophorus* (p. 364).

Giebel, C. G.

1855. Die Säugethiere. (Leipzig, Abel), xii + 1108.

Haplodon referred to the family Spalacini; the genus *Haplodon* (p. 526); *H[aplodon]. leporinus* (p. 527).

1859. Die Naturgeschichte des Thierreichs. I. Die Säugethiere. (Leipzig, Wigand), viii + 522 pp., 926 figs. in text.

Reference made to *Haplodon leporinus* in account of genus *Georhychus;* skull figured (p. 279).

Gill, T.

1872. Arrangement of the families of mammals with analytical tables. Smithson. Misc. Coll., **11**, vi + 98.

Haploodontidae listed as sole family under superfamily Haploodontoidea (p. 22).

Gray, J. E.

1843. List of the specimens of mammalia in the collection of the British Museum. (London, British Museum), xxviii + 216 pp.
Three skins of the Sewellel, *Aplodontia leporina*, from "N. America," are in the collection (p. 150).

Griffith, E.

1827. The animal kingdom. (London, Whittaker), **5**, 1–391.
Reference to *A[rctomys]. rufa* (p. 245).

Grinnell, J.

1913. A distributional list of the mammals of California. Proc. Calif. Acad. Sci. (4), **3**, 265–390, pls. 15, 16.
Two species of *Aplodontia—A. californica* and *A. phaea*—listed as occurring in California (p. 344).

1915. The vertebrate fauna of the Pacific Coast, *in* Nature and science on the Pacific Coast. (San Francisco, Elder), pp. 104–114, pls. 12–14.
Aplodontia mentioned (p. 110); photograph of live animal (pl. 14, opp. p. 118).

1916. An analysis of the vertebrate fauna of the Trinity region of northern California. Univ. Calif. Publ. Zool., **12**, 399–410.
In course of analysis mentions *A[plodontia]. californica* (p. 401), and *Aplodontia chryseola* (pp. 401, 402, 407).

Harlan, R.

1825. Fauna Americana. (Philadelphia, Finley), pp. i–x, 11–318.
Compilation of matter on *Arctomys rufa* (addenda, pp. 308–309).

Holder, J. B.

1877. History of the American Fauna, in the Museum of Natural History. (New York, Virtue), pp. i–cexc, 11 pls.
Short compilation; treats family Haplodontidae, genus *Haplodon* and the species *Haplodon rufus* (p. xc).

Kellogg, L.

1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. Univ. Calif. Publ. Bull. Dept. Geol., **5**, 421–437, 20 figs. in text.
Aplodontia alexandrae briefly discussed (p. 429).

1912. Pleistocene rodents of California. Univ. Calif. Publ. Bull. Dept. Geol., **7**, 151–168, 16 figs. in text.
Discussion of *Aplodontia major fossilis* from Samwel and Potter Creek caves in California (pp. 157–158); incidental mention of *Aplodontia major* (p. 158).

1914. *Aplodontia chryseola*, a new mountain beaver from the Trinity region of northern California. Univ. Calif. Publ. Zool., **12**, 295–296.
Original description of *Aplodontia chryseola*.

1916. Report upon mammals and birds found in portions of Trinity, Siskiyou and Shasta counties, California. Univ. Calif. Publ. Zool., **12**, 335–398, pls. 15–18, 1 fig. in text.
Relationships, occurrence and habits of *Aplodontia chryseola* (pp. 369–372).

Lantz, D. E.

1917. Destroying rodent pests on the farm. Yearbook, U. S. Dept. Agr., Separate 708 (1916), 1–18, 5 pls., 1 fig. in text.

Damage done by aplodontia to crops in western Washington mentioned (p. 16); half-tone of aplodontia (plate 1, fig. 1).

Lesson, R. P.

1827. Manuel de mammalogie ou histoire naturelle des mammifères(Paris, Roret), xv + 442 pp.

Short paragraph on *Anisonyx rova* (p. 240); evidently compiled from Rafinesque and Harlan.

Lewis, M., and Clark, W.

1814. History of the Lewis and Clark Expedition. (Paul Allen edition, Philadelphia, Bradford), 2, ix + 522.

Description of "Sewellel" (pp. 176–177).

1876. An account of the various publications relating to the travels of Lewis and Clark, with a commentary on the zoological results of their Expedition; Elliott Coues, *in* U. S. Geol. and Geog. Surv. Terr. (2), Bull. 6, 417–444.

Short compilation regarding the Sewellel (p. 437).

1893. History of the Expedition under the command of Lewis and Clark. 4 vols. (Coues edition, New York, Harper), 3, i–vi, 821–1298.

Extract on the Sewellel from the journals of Lewis and Clark (pp. 861–862); critical remarks (footnote, p. 861).

1904–5. Original journals of the Lewis and Clark Expedition, 1804–1806. 8 vols. (Thwaites' edition, New York, Dodd), 8 [Atlas], i–xvi, 54 maps.

Parts 1 and 2 of map 32 are of particular interest as showing the localities on the Columbia River visited by Lewis and Clark.

Lilljeborg, W.

1866. Systematisk öfversigt af de gnagande Däggdjuren, Glires. (Upsala, Kongl. Akad. Boktryckeriet), pp. 1–59.

Family Haploodontidae placed between Sciuridae and Chinchillidae in table, opp. p. 9; family discussed (p. 41).

Lord, J. K.

1866. The naturalist in Vancouver Island and British Columbia. 2 vols. (London, Bentley), 1, xiv + 358, frontisp., 6 illus. in text.

Chapter 13 devoted to discussion of habits, Indian names, and distribution of *Aplodontia leporina*.

Lum, S. K.

1878. The sewellel or show'tl. Amer. Nat., 12, January, 10–13.

Remarks on distribution and habits of *Haplodon rufus*.

[Lydekker, R.]

1914. Guide to the galleries of Mammals in the Department of Zoology of the British Museum (Natural History), (ed. 9, London, British Museum), 123 pp., 1 pl., 3 plans, 65 figs. in text.

Reference to Aplodontiidae and the genus *Aplodontia* (p. 57).

Lyon, M. W., Jr.

1907. Notes on mammals collected at Mount Rainier, Washington. Smithsonian Misc. Coll., 50, 89–92.

Aplodontia major rainieri discussed (p. 91).

Lyon, M. W., Jr., and Osgood, W. H.

1909. Catalogue of the type-specimens of mammals in the U. S. National Museum, including the Biological Survey collection. U. S. Nat. Mus., Bull. 62, x + 325.

The types of three forms of *Aplodontia* were in the Biological Survey Collection on the date of publication of this catalogue, as follows: *Aplodontia olympica, A. pacifica,* and *A. major rainieri* (pp. 159–160).

Marsh, O. C.

1877. New vertebrate fossils. Amer. Jour. Sci. (3), 14, 249–256.

Original description of the genus *Allomys* (p. 253).

Matteson, F. S.

1877. The mountain boomer, or showtl. Amer. Nat., 11, 434–435.

Letter regarding habits of aplodontia.

Matthew, W. D., and Gidley, J. W.

1904. New or little known mammals from the Miocene of South Dakota. Amer. Mus. Exp. 1903. Bull. Amer. Mus. Nat. Hist., 20, 241–268, 15 figs. in text.

Meniscomys sp. indt., recovered in Rosebud beds; comparison of *Meniscomys* with *Haplodontia* (pp. 263, 264).

Matthew, W. D.

1907. A Lower Miocene fauna from South Dakota. Bull. Amer. Mus. Nat. Hist., 23, 169–219, 26 figs. in text.

Meniscomys sp. listed from Lower Rosebud (p. 172).

1910. On the osteology and relationships of *Paramys,* and the affinities of the Ischyromyidae. Bull. Amer. Mus. Nat. Hist., 38, 43–72, 19 figs. in text.

Aplodontia and the Aplodontiidae considered in comparison and treatment of primitive rodents (pp. 44, 47, 48, 64–69, 71).

Merriam, C. H.

1886. Description of a new species of Aplodontia (*Aplodontia major,* sp. nov.) from California. Ann. N. Y. Acad. Sci., 3, no. 10, pp. 312–328, 2 pls., 1 fig. in text.

Description of *Aplodontia major,* including discussion of history, nomenclature, habits, and variation.

1897. The mammals of Mount Mazama, Oregon. Mazama, 1, 204–230.

Habits of *Aplodontia major* as observed on Mount Mazama, near Crater Lake (p. 219).

1899*a*. Descriptions of six new rodents of the genera *Aplodontia* and *Thomomys.* Proc. Biol. Soc. Wash., 13, 19–21.

Original descriptions of *Aplodontia pacifica, A. phaea, A. olympica,* and *A. major rainieri.*

1899*b*. Results of a biological survey of Mount Shasta, California. U. S. Dept. Agr., Div. Biol. Surv., N. Amer. Fauna, 16, 1–179, pls. 1–5, 46 figs. in text.

Aplodontia major rainieri listed as a Cascade species (pp. 74, 81); occurrence and habits of *Aplodontia major* on Mt. Shasta (pp. 92, 93).

Merriam, J. C.

1911. Tertiary mammal beds of Virgin Valley and Thousand Creek in northwestern Nevada. Part II, Vertebrate faunas. Univ. Calif. Publ. Bull. Dept. Geol., 6, 199–304, pls. 32–33, 80 figs. in text.

Aplodontia alexandrae listed from Virgin Valley (p. 205); from Thousand Creek (p. 211).

1916. Tertiary vertebrate fauna from the Cedar Mountain region of western Nevada. Univ. Calif. Publ. Bull. Dept. Geol., 9, 161–198, pl. 8, 48 figs. in text.

Aplodontia sp. from the Upper Miocene described (pp. 177–179).

Merriam, J. C., and Sinclair, W. J.

1907. Tertiary faunas of the John Day region. Univ. Calif. Publ. Bull. Dept. Geol., 5, 171–205.

Four species of *Allomys* from the John Day beds are assigned to the Haplodontidae (p. 185).

Miller, G. S., Jr.

1912. List of North American land mammals in the U. S. National Museum, 1911. U. S. Nat. Mus., Bull. 79, xiv + 455.

Six forms of *Aplodontia* listed, as follows: *Aplodontia major major*, *A. m. rainieri*, *A. olympica*, *A. pacifica*, *A. phaea*, *A. rufa* (p. 291).

Miller, G. S., Jr., and Rehn, J. A. G.

1901. Systematic results of the study of North American land mammals to the close of the year 1900. Proc. Bost. Soc. Nat. Hist., 30, 1–352.

Six forms of *Aplodontia* listed, as follows: *Aplodontia major*, *A. m. rainieri*, *A. olympica*, *A. pacifica*, *A. phaea*, *A. rufa* (pp. 63–64).

Minding, J.

1829. Ueber die geographische Vertheilung der Säugethiere. (Berlin, Enslin), pp. 1–104.

Refers genus *Anisonix* [= *Anisonyx* = *Aplodontia* (part)] to family Prensiculantia; genus includes species *brachyura* and "*rufa?*" (p. 86).

Muir, J.

1909. Our national parks. (Boston, Houghton), x + 382 pp., numerous unnumbered plates.

Reference to *Haplodon* (p. 201).

Murphy, J. M.

1876. The hunting fields of the Pacific Coast. Capturing the showtl. Rod and Gun, May 20, p. 121.

Habits of *Aplodontia leporina*.

1877. The shewelel or showtl. London Field, April 28, 486–487.

Habits of *Aplodontia leporina*.

Murray, A.

1866. The geographical distribution of mammals (London, Murray), xvi + 420 pp., 101 maps, numerous figs in text, numbered separately under chapters.

Reference to classification and habits of *Aplodontia leporina* (p. 263); additional references (pp. 356, 399, 401).

Newberry, J. S.

1857. Report upon the mammals, *in* Zoological Report, *in* U. S. Pac. R. R. Expl. and Surv., **6**, 35–72, 3 pls.

Remarks on distribution of *Aplodontia leporina* (p. 58).

Osborn, H. F.

1910. The age of mammals in Europe, Asia and North America. (New York, Macmillan), xvii + 635 pp., 220 figs. in text.

Superfamily Aplodontoidea; also family Aplodontiidae with three genera, *Meniscomys*, *Mylagaulodon*, *Aplodontia*, listed (p. 534).

Palmer, T. S.

1904. Index generum mammalium: a list of the genera and families of mammals. U. S. Dept. Agr., Div. Biol. Surv., N. Amer. Fauna, **23**, pp. 984.

Possible variations in generic name *Aplodontia* discussed (p. 25); genus *Aplodontia* (pp. 112–113); family names considered (pp. 744, 782, 841–842).

Peale, T. R.

1848. Mammalia and ornithology. U. S. Expl. Exp. (Wilkes) (Philadelphia, Sherman), **8**, i–xxvi, 17–338, several unnumbered figs. in text.

Aplodontia leporina discussed, and skull figured (pp. 56–57).

Peters, W.

1864. Neue Arten der Säugethiergattungen *Geomys*, *Haplodon*, und *Dasypus*. Mon. k. preuss. Akad. Wiss. Berlin, **1864**, 177–180.

Original description of *H[aplodon]. leporinus* var. *californicus*.

Price, W. W.

1894. Notes on a collection of mammals from the Sierra Nevada Mountains. Zoe, **4**, 315–332.

Habits and distribution of *Aplodontia major* (p. 328).

Rafinesque, C. S.

1817. Descriptions of seven new genera of North American quadrupeds, *in* Museum of Natural Sciences, *in* Amer. Monthly Mag. and Crit. Rev., **2**, 44–46.

Original description of "*Anisonyx? rufa*" (p. 45).

Richardson, J.

1829*a*. On Aplodontia, a new genus of the order Rodentia, constituted for the reception of the sewellel, a burrowing animal which inhabits the northwestern coast of America. Zool. Jour., **4**, 333–337.

Original description of genus, and of species *leporina*.

1829*b*. Fauna Boreali-Americana. (London, Murray), Part I, xlvi + 300 pp., 28 pls.

Descriptive remarks; genus *Aplodontia* (p. 210); species *leporina* (pp. 211–213); cranium, foot, and tooth figured (figs. 7–14, pl. 18C, opp. p. 197).

1837. Report on North American zoology, *in* Rep. 6th meeting Brit. Assoc. Adv. Sci., **5**, 121–224.

Aplaodontia leporina listed (p. 150).

Schinz, H.

1845. Synopsis Mammalium (Solothurn, Jent), **2**, 1–574.

Compiled account of *Aplodontia leporina* (pp. 138–139).

Schlosser, M.

1884. Die Näger des europäischen Tertiärs. Palaeontographica, **31**, 19–161, 16 numbered, several unnumbered, figs. in text, pls. 5–12.

Abstract of Winge's Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien, E. Museo Lundii, *in* Verzeichniss der anthropologischen Literatur, Archiv. f. Anthrop., **19**, 89–90.

Haplodontidae and *Haplodon* mentioned (p. 89); *Haplodon* (p. 90).

Scott, W. B.

1913. A history of land mammals in the western hemisphere (New York, Macmillan), xiv + 693 pp., frontisp., 304 figs. in text.

Aplodontia rufa mentioned (pp. 153, 233); Aplodontiidae (p. 249).

Sinclair, W. J.

1903. A preliminary account of the exploration of the Potter Creek Cave, Shasta County, California. Science, n.s., **17**, 708–712.

"*Aplodontia* either a new species or a new subspecies of *A. major*" listed (p. 711).

1905. New mammalia from the quaternary caves of California. Univ. Calif. Publ. Bull. Dept. Geol., **4**, 145–161, pls. 19–23, 2 figs. in text.

Original description of *Aplodontia major fossilis* (p. 147).

Stephens, F.

1906. California mammals. (San Diego, West Coast Publishing Co.), 351 pp., frontisp., many unnumbered figs. in text.

Family Aplodontidae, genus *Aplodontia*, and two species, *major* and *phaea*, discussed (pp. 93–95).

Stone, W., and Cram, W. E.

1902. American animals. (New York, Doubleday), xxiii + 318 pp., many unnumbered illustrations.

Family Aplodontidae and species *Aplodontia rufa* discussed (pp. 150–151).

Suckley, G.

1860. Report, *in* Zool. Rep., U. S. Pac. R. R. Expl. and Surv., **12**, bk. 2, pt. 3, no. 2, chap. 2, pp. 89–106.

Remarks on, and description and habits of, *Aplodontia leporina* (p. 100).

Suckley, G., and Gibbs, G.

1860. *Op. cit.*, chap. 3, pp. 107–139, pls. 2, 5, 7, 9, 15.

Distribution of *Aplodontia leporina;* habits, Indian traditions (pp. 124–126).

Swainson, W.

1835. On the natural history and classification of quadrupeds. (London, Longmans), viii + 397 pp., 176 figs. in text.

Aplodontia (genus) discussed; *Ap[lodontia]. leporina* mentioned (p. 388).

Taylor, W. P.

1914. A previously undescribed *Aplodontia* from the middle north coast of California. Univ. Calif. Publ. Zool., **12**, 297–300.

Original description of *Aplodontia nigra*.

1916*a*. *Aplodontia humboldtiona:* a new mountain beaver from the Humboldt Bay district, California. Proc. Biol. Soc. Wash., **29**, 21–24.

Original description of *Aplodontia humboldtiona*.

1916*b*. The status of the beavers of western North America, with a consideration of the factors in their speciation. Univ. Calif. Publ. Zool., **12**, 413–495, figs. A–Q in text.

Paragraph on the Aplodontiidae (pp. 470, 471).

1916*c*. Two new aplodontias from western North America. Univ. Calif. Publ. Zool., **12**, 497–501.

Original descriptions of *Aplodontia rufa grisea* (p. 497), and *Aplodontia californica columbiana* (p. 499).

Thomas, O.

1896. On the genera of rodents: an attempt to bring up to date the current arrangement of the order. Proc. Zool. Soc. London, **1896**, 1012–1028.

Places *Anomalurus* and *Aplodontia* in groups by themselves, specifically providing that their true relationships will have to be shown by further research (p. 1014).

Townsend, C. H.

1887. Field-notes on the mammals, birds and reptiles of northern California. Proc. U. S. Nat. Mus., **10**, 159–241.

Discussion of *Haplodon rufus* (pp. 174–175); mention made of *H. major* (footnote, p. 174).

Trouessart, E. L.

1897. Catalogus mammalium tam viventium quam fossilium. (Berlin, Friedländer), tome 1, fasc. 2, pp. 219–452.

Lists two species of *Aplodontia*, namely [*Aplodontia*] *rufa* and [*Aplodontia*] *major* (p. 450).

1904. Catalogus mammalium tam viventium quam fossilium. Quinquenalle supplementum: Rodentia, fasc. 2, pp. 289–546.

Lists seven forms of *Aplodontia*, namely [*Aplodontia*] *rufa* [*A. r.*] *californica*, [*A. r.*] *rainieri*, [*A.*] *pacifica*, [*A.*] *phaea*, [*A.*] *olympica*, [*A.*] *major* (p. 348).

True, F. W.

1885. A provisional list of the mammals of North and Central America, and the West Indian Islands. Proc. U. S. Nat. Mus., **7**, App., 587–611.

Reference to family Haplodontidae and to *Haplodon rufus* (p. 596).

Tullberg, T.

1896. Zur Anatomie des *Haplodon rufus*. Zooliska Studier (Upsala, Almquist), pp. 231–251, 2 pls.

Anatomy and remarks on classification (p. 250).

Wagler, J.

1830. Natürliches System der Amphibien mit vorangehender Classification der Säugethiere und Vögel (Mnnich, Cotta), vi + 354 pp., 2 tables.

Haplodon listed (p. 4); sewellel (p. 22).

Wagner, J. A.

1843. Die Säugethiere [Schreber]. Supplementband, **3**. Abt., pp. xiv + 614.

Haplodon characterized; *Haplodon leporinus* discussed (pp. 395–396).

WALLACE, A. R.

1876. The geographical distribution of animals. 2 vols. (London, Macmillan), **2**, viii + 607, 2 maps, 7 pls.

WEBER, M.

1904. Die Säugetiere (Fischer, Jena), xi + 866 pp., 567 figs. in text.
Aplodontia referred to "Familie" Haplodontoidea (p. 496).

WINGE, H.

1888. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E. Museo Lundii., **3**, 1–200, pls. 1–8.
Haplodontidae (pp. 108, 110, 115, 135, 189); *Haplodon* (pp. 108, 115, 164, 189); relationships of rodent families (p. 110); Haplodontidae thought to be derived from Ischyromyidae, and Anomaluridae and Sciuridae derived from Haplodontidae.

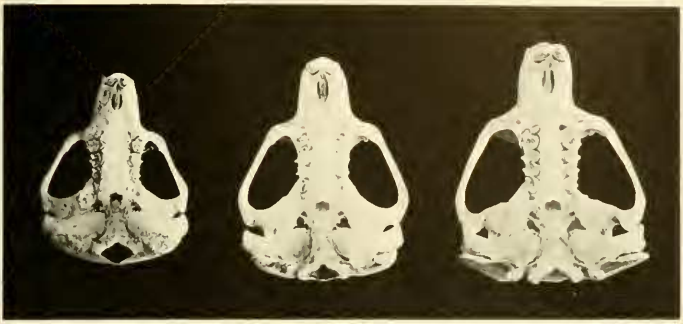
ZITTELL, K. A.

1894. Traité de paléontologie. 1. Paleozoologie: 4. Vertebrata; mammalia. (Paris, Doin), xi + 806 pp., 591 figs. in text.
Haplodontidae referred to Protrogomorpha (p. 523).

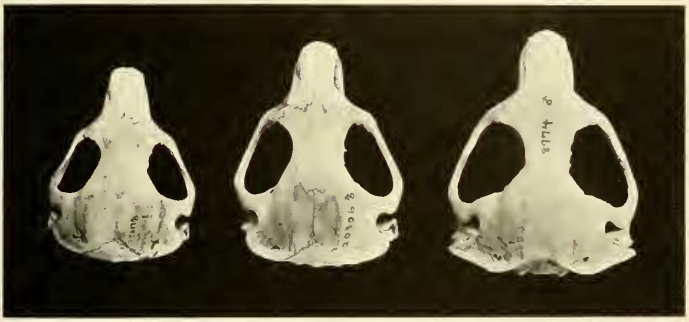
EXPLANATION OF PLATE 25

Crania of *Aplodontia rufa phaea*, to show some of the changes which take place with age; × 0.67. Figs. 1*a*, 1*b*, 1*c*, no. 20317, Mus. Vert. Zool.; figs. 2*a*, 2*b*, 2*c*, no. 20306, Mus. Vert. Zool.; figs 3*a*, 3*b*, 3*c*, no. 8974, Mus. Vert. Zool.

Note in the crania dorsally the disproportionate expansion of the skull, particularly posteriorly; the marked reduction in width of the interorbital constriction; and the disappearance of sutures. In the crania ventrally note the increase in measurements, the disappearance of sutures, and the disproportionate lateral growth of the mastoid processes as compared with the audital tubes; but note that the distance across the palate between the fourth premolars remains nearly constant. In posterior view note the disproportionately rapid outgrowth of the mastoid processes, with consequent disappearance of audital tubes, the change in outline of the foramen magnum, and the change in outline of the entire posterior aspect of the cranium, due to the development of the lambdoidal ridges and the outgrowth of the mastoid processes.



1*a* 2*a* 3*a*



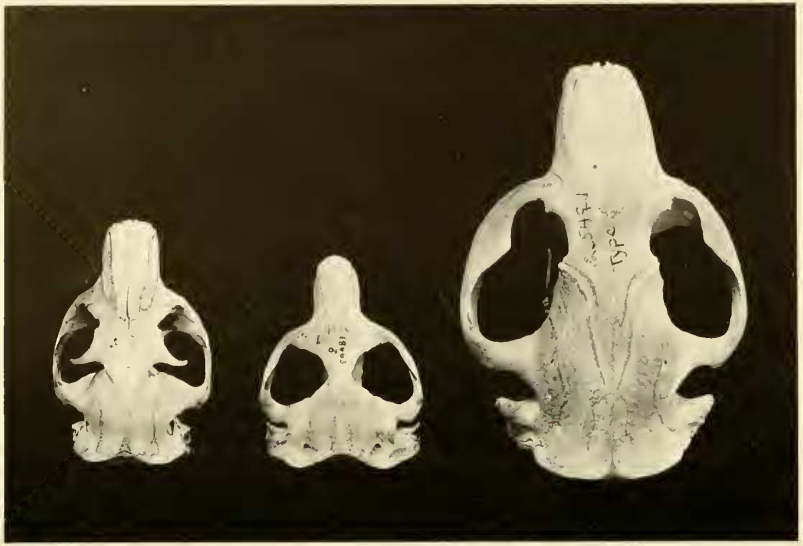
1*b* 2*b* 3*b*

1*c* 2*c* 3*c*

EXPLANATION OF PLATE 26

Dorsal view of crania of woodchuck, aplodontia, and beaver; all × 0.50. Fig. 4, *Marmota flaviventris sierrae*, no. 15165, Mus. Vert. Zool.; fig. 5, *Aplodontia rufa californica*, no. 18663, Mus. Vert. Zool.; fig. 6, *Castor subauratus subauratus*, no. 12654, Mus. Vert. Zool.

Note in *Aplodontia* and *Castor* the absence of postorbital processes on the frontal; also the comparative width of the cranium posteriorly in *Aplodontia*, as compared with *Marmota* and *Castor*.



4 5 6

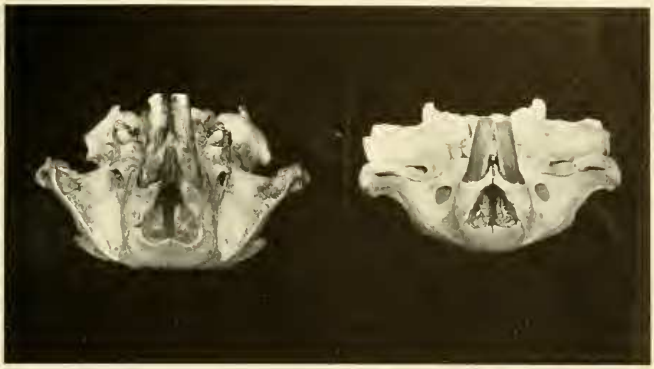
EXPLANATION OF PLATE 27

Figs. 7, 8.—Anterior view of crania of sciurid type and aplodontid type, to illustrate difference in infraorbital arrangement; × 0.77. Fig. 7, *Marmota flaviventris sierrae*, no. 15165, Mus. Vert. Zool.; fig. 8, *Aplodontia rufa californica*, no. 18663, Mus. Vert. Zool.

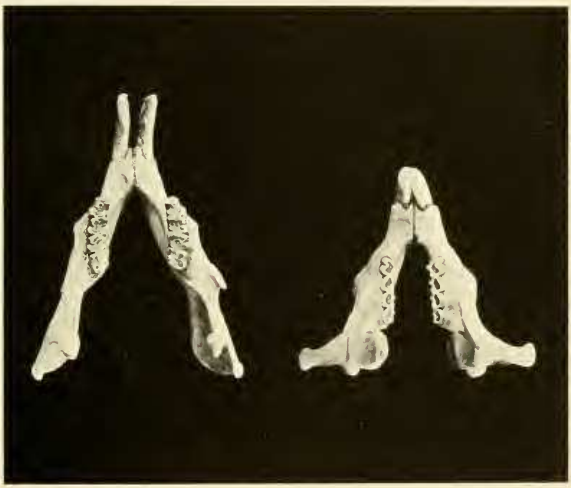
Note in *Marmota* the broadly expanded fossa for the masseter muscle just laterad of the infraorbital foramen on either side; note also the compression and reduction in size of the infraorbital foramen in this genus; note, on the other hand, the generalized character of the region in *Aplodontia*, there being no provision for the masseter muscle anterior of the ventral border of the anterior root of the zygomatic arch, and the infraorbital foramen being comparatively large, much as in the Eocene rodent family Ischyromyidae.

Figs. 9, 10. Dorsal view of mandibles of aplodontid and sciurid, to illustrate different development of angular processes; × 0.66. Fig. 9, *Marmota flaviventris sierrae*, no. 15165, Mus. Vert. Zool.; fig. 10, *Aplodontia rufa californica*, no. 18663, Mus. Vert. Zool.

Note the lateral expansion of the angle in *Aplodontia* as compared with *Marmota*.



7 8

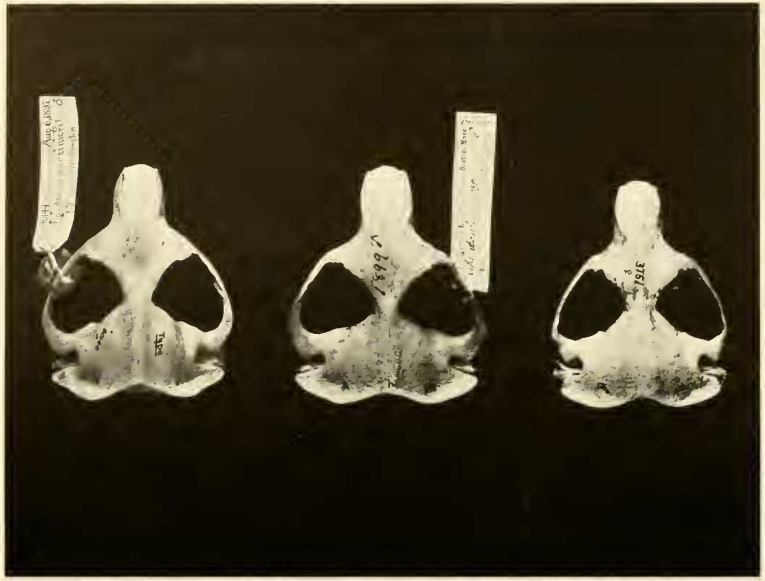


9 10

EXPLANATION OF PLATE 28

Dorsal view of crania of three subspecies of *Aplodontia;* × 0.54. Fig. 11, *Aplodontia rufa rainieri,* no. 90144, Biol. Surv. Coll.; fig. 12, *Aplodontia rufa columbiana,* no. 1899, Mus. Comp. Zool.; fig. 13, *Aplodontia rufa rufa,* no. 3751, Mus. Vert. Zool.

Note the general similarity in size between *Aplodontia rufa rainieri* and *A. r. columbiana,* with the latter somewhat the larger; note the heavier zygomatic arch in *columbiana* as compared with either of its neighbors, together with the greater expansion of the arch near the posterior root. Note the tendency in *rainieri* and *columbiana* to have temporal ridges closer together than in *Aplodontia rufa rufa.* Note in the latter the general smaller size and lighter zygomatic arch as compared with the mountain subspecies.



11 12 13

EXPLANATION OF PLATE 29

Study of fresh specimen of *Aplodontia rufa californica;* male, no. 22618, Mus. Vert. Zool.; East Fork Indian Cañon, Yosemite National Park, California; June 19, 1915; × 0.35.

Note the small ear with white spot at base, the short tail, the chunky body and blunt head.